Population and community responses along environmental gradients across spatio-temporal scales

Dissertation von Nicolas Alexander Konstantin Frieß

Philipps-Universität Marburg

März 2019

Population and community responses along environmental gradients across spatio-temporal scales

Dissertation

zur

Erlangung des Doktorgrades der Naturwissenschaften

(Dr. rer. nat.)

dem Fachbereich Biologie

der Philipps-Universität Marburg

vorgelegt von

Nicolas Alexander Konstantin Frieß

aus Frankfurt am Main

Marburg an der Lahn, März 2019

Vom Fachbereich Biologie der Philipps-Universität Marburg
als Dissertation am 17.05.2019 angenommen.

Erstgutachter: Prof. Dr. Roland Brandl
Zweitgutachterin: Prof. Dr. Nina Farwig

Tag der mündlichen Prüfung am 27.06.2019

Table of Contents

Table of Contents

Summary

Ecology as a science investigates organisms in interaction with their environment. This thesis aims at investigating how the environment and species' traits as well as their interaction affect population and community structure and dynamics on varying spatial and temporal scales. In order to derive predictions of how ecological communities will respond to ongoing environmental change we need to understand (I) community responses to environmental gradients and their variation, (II) drivers of species' performances and (III) how species' traits affect species' success in a particular environment. After a general introduction in chapter 1, I investigate these questions in seven articles subdivided in three chapters.

Chapter 2 focusses on the response of ecological communities in terrestrial forest ecosystems to environmental conditions changing along natural gradients. Here, I show the strong effect of a local elevational gradient and the associated changes in environmental conditions on alpha and beta diversity of a multi-taxon community. Additionally, I analyze how organisms of varying taxonomic groups and trophic levels respond to temperate forest succession and the associated changes in forest structural parameters. Finally, I investigate how climatic conditions, geographic space and forest structure affect alpha and beta diversity of fungus-dwelling arthropod communities on a continental scale. The results reveal strong differences in the response to changing environmental conditions among taxonomic and trophic groups, underline the importance species turnover across successional stages for the regional species pool and reveal that climatic conditions and geographic space may play only minor roles in particular communities like those inhabiting fungus fruiting bodies.

In chapter 3, I investigate how species' performances are affected by species traits. Here, I test several proposed hypotheses aimed at explaining the ubiquitous relationship between local distribution and mean abundance in a causal statistical framework. For phytophagous insects I show that habitat availability is the most important driver of local distribution which in turn facilitates species' mean abundances via population dynamic processes. This relationship is further modulated by species' energy uptake and allocation strategies. Species that successfully compensate for higher energetic costs associated with beneficial morphological traits may reach higher local distributions and mean abundances.

Chapter 4 aims at investigating how the effect of a particular trait on species' success may change with changing environmental conditions. Here, two studies investigate the effect of thermoregulatory relevant functional traits on the occurrence of moth along changing thermal conditions along spatial gradients. The results show that the relationship between species' traits and species' performances is highly context and scale dependent, as the presented studies revealed strong intra- and intertaxonic differences in the trait-environment relationships.

Identifying important environmental gradients driving community dynamics (I), determining the drivers of species' performances (II) and analyzing the interactive effect of environment and traits on species' performances across scales (III) as pursued in this thesis helps us to identify the relevant drivers of species responses to environmental change on particular spatio-temporal scales for particular communities. Furthermore, these insights broaden our knowledge of the processes generating and maintaining terrestrial biodiversity. However, the results also show that it is debatable whether it is possible in the near future to generate reliable and more importantly generalizable predictions of how future environmental change will affect terrestrial communities as a whole.

Zusammenfassung

Die wissenschaftliche Ökologie untersucht Organismen in Wechselwirkung mit ihrer Umwelt. Um Vorhersagen ableiten zu können, wie ökologische Gemeinschaften in der Zukunft auf fortschreitende Umweltveränderungen reagieren werden, ist es notwendig zu verstehen wie (I) Artengemeinschaften allgemein auf sich natürlich ändernde Umweltbedingungen reagieren, (II) welche Merkmale für den Erfolg von Arten verantwortlich sind und (III) wie Merkmale den Erfolg einer Art in Abhängigkeit von gegebenen Umweltbedingungen beeinflussen. Nach einer generellen Einleitung in Kapitel 1, untersuche ich diese Fragestellungen in dieser Arbeit anhand von sieben Fachartikeln unterteilt in drei Kapiteln.

Kapitel 2 untersucht die Reaktion von Artengemeinschaften auf sich ändernde Umweltbedingungen entlang natürlicher Gradienten in terrestrischen Waldökosystemen Hierbei zeige ich den starken Effekt lokaler Höhengradienten und der damit assoziierten Änderung der Umweltbedingungen auf die Alpha- und Beta-Diversität von Artengemeinschaften verschiedener Organismengruppen. Weiterhin analysiere ich wie Organismen verschiedener Taxa und trophischer Ebenen auf sich ändernde Waldstrukturparameter verschiedener Sukzessionsstadien reagieren. Schließlich untersuche ich wie klimatische, geographische und waldstrukturelle Bedingungen die Diversität von Arthropodengemeinschaften auf kontinentaler Skala beeinflussen. Die Ergebnisse zeigen starke Unterschiede in der Reaktion auf sich ändernde Umweltbedingungen zwischen taxonomischen und trophischen Gruppen auf, unterstreichen die Bedeutung des Artenumsatzes zwischen Sukzessionsstadien für den regionalen Artenpool und offenbaren das für bestimmte Artengemeinschaften, wie die in Pilzfruchtkörpern lebenden Arthropoden, Klimabedingungen und der geographische Raum nur eine untergeordnete Rolle spielen.

Im Kapitel 3 untersuche ich wie der Erfolg von Arten durch deren Merkmale beeinflusst werden. Dabei teste ich verschiedene Hypothesen die zur Erklärung der allgegenwärtigen Beziehung zwischen lokaler Verbreitung und mittlerer Abundanz aufgestellt wurden. Anhand phytophager Insekten demonstriere ich das die Habitatverfügbarkeit in der Landschaft der wichtigste Faktor für die lokale Verbreitung und im Folgeschluss auch für die mittlere Abundanz der Tiere ist. Diese Beziehung wird weiterhin durch energetische Strategien der Arten moduliert.

Kapitel 4 untersucht wie sich positive Effekte von Arteigenschaften auf den Erfolg der Arten verändern, wenn sich die Umweltbedingungen ändern. Zwei Studien untersuchen hier den Effekt von thermoregulatorisch relevanten Merkmalen auf die Verbreitung von Nachtfaltern entlang von Temperaturgradienten. Starke inter- und intrataxonische Unterschiede in den Merkmals-Umwelts-Beziehungen deuten hierbei darauf hin, dass derlei Beziehungen stark von der Skala und dem Kontext der Untersuchung abhängen.

Die Identifikation relevanter Umweltgradienten, welche die Dynamik von Artengemeinschaften beeinflussen (I), die Bestimmung relevanter Arteigenschaften welche den Erfolg oder Misserfolg von Organismen bestimmen (II) sowie die Analyse der interaktiven Auswirkungen dieser Umweltbedingungen und Arteigenschaften auf das Vorkommen von Arten (III) wie sie in dieser Arbeit präsentiert wurde können uns helfen relevanten Treiber für bestimmte Arten und Artengemeinschaften in bestimmten raum-zeitlichen Kontexten zu identifizieren Darüber hinaus erweitern diese Erkenntnisse unser Wissen über die Prozesse, die die terrestrische Biodiversität erzeugen und erhalten. Die Ergebnisse zeigen jedoch auch, dass es fraglich ist, ob es in naher Zukunft möglich ist, verlässliche und vor allem verallgemeinerbare Vorhersagen darüber zu generieren, wie zukünftige Umweltveränderungen die terrestrischen Gemeinschaften insgesamt beeinflussen werden.

List of publications used in this thesis

Chapter 2.1

Friess, N., C. Bässler, R. Brandl, T. Hilmers, J. Müller, and L. Seifert. 2018. Biodiversity along an elevational gradient of the Bohemian Forest – the BIOKLIM project. Silva Gabreta 24:149–160.

Chapter 2.2

Hilmers, T., **N. Friess**, C. Bässler, M. Heurich, R. Brandl, H. Pretzsch, R. Seidl, and J. Müller. 2018. Biodiversity along temperate forest succession. Journal of Applied Ecology 55:2756–2766.

Chapter 2.3

Friess, N., J. C. Müller, P. Aramendi, C. Bässler, M. Brändle, C. Bouget, A. Brin, H. Bussler, K. B. Georgiev, R. Gil, M. M. Gossner, J. Heilmann-Clausen, G. Isacsson, A. Krištín, T. Lachat, L. Larrieu, E. Magnanou, A. Maringer, U. Mergner, M. Mikoláš, L. Opgenoorth, J. Schmidl, M. Svoboda, S. Thorn, K. Vandekerkhove, A. Vrezec, T. Wagner, M.-B. Winter, L. Zapponi, R. Brandl, and S. Seibold. 2019. Arthropod communities in fungal fruitbodies are weakly structured by climate and biogeography across European beech forests. Diversity and Distributions 25:783-796.

Chapter 3.1

Friess, N., M. M. Gossner, W. W. Weisser, R. Brandl, and M. Brändle. 2017. Habitat availability drives the distribution–abundance relationship in phytophagous true bugs in managed grasslands. Ecology 98:2561–2573.

Chapter 3.2

Pinkert, S., **N. Friess**, D. Zeuss, M. M. Gossner, R. Brandl, and S. Brunzel. In preparation. Mobility costs and energy uptake modulate the occurrence of butterflies. Under Consideration by Nature Communications.

Chapter 4.1

Heidrich, L., **N. Friess**, K. Fiedler, M. Brändle, A. Hausmann, R. Brandl, and D. Zeuss. 2018. The dark side of Lepidoptera: Colour lightness of geometrid moths decreases with increasing latitude. Global Ecology and Biogeography 27:407–416.

Chapter 4.2

Friess, N., L. Heidrich, S. Pinkert, N. Roth, J. Müller, and R. Brandl. In preparation. A local elevational gradient in the body size and color lightness of nocturnal insects: contrasting strategies among noctuid and geometrid moths.

Chapter 1

General Introduction

Ecological organization and processes

Ecology as a science investigates organisms in interaction with their environment. Organisms reproduce, disperse, survive or grow, thereby forming local populations with specific dynamics of births and deaths. These populations persist or perish due to stochastic as well as deterministic processes (Begon et al. 1996). Individuals again emigrate from these populations and immigrate into others with distinct rates, forming metapopulations (Hanski 1999). Over the course of natural history, evolutionary processes including speciation, gene flow, drift and selection lead to a diversity of different types of organisms, called species (Hartl and Clark 2006). At every point in space and time populations of several species occur together with the potential for interaction, forming ecological communities (Morin 2011). Communities themselves gain species either over time *via* speciation (Nowak 2006) or *via* dispersal, by migration from other communities, forming metacommunities (Holyoak et al. 2005, Cadotte 2006). Communities may lose species stochastically by ecological drift as there is always a non-zero probability for populations in a community to go locally extinct (Hubbell 2001). Furthermore, communities may lose species deterministically as the result of relative fitness differences of species given the present environmental conditions, called selection (Vellend 2010, 2016).

All ecological processes can be traced back to the individual organism interacting with its environment. The probabilities and rates of the high-level processes dispersal, reproduction, survival or growth depend on the traits of the individual – i.e. any proxy for organismal performance (Darwin 1859) – and the environmental conditions it is confronted with. A particular trait increases the fitness of an organism in a given environment if it increases the probability of success or the rate of one of the aforementioned processes (Sober 2000). An increase of the probability of success reduces the probability of failure and thus, in the long term, the rate of ecological drift (Vellend 2016). Relative fitness differences among individuals may lead to the fixation of a trait in a population (Nowak 2006), while the relative fitness differences among populations of different species may lead to a deterministic change in community composition in terms of relative frequencies of species (Vellend 2016). The acknowledgment of the importance of traits for ecological processes led to the rise of trait-based approaches in community ecology and the emphasize on functional traits, i.e. traits that increase the relative fitness of a species (McGill et al. 2006, Violle et al. 2007).

In this context, the popular metaphor of environmental filtering conveys the view that environmental conditions act as a selective force that allows some species to establish and persist while others won't (Kraft et al. 2015). Species depending on oxygen, for instance, will perish under anaerobic conditions while anaerobic bacteria might thrive. Yet, not always will the environment directly 'filter out' certain traits or associated species, especially as environmental conditions vary gradually on small spatial or temporal scales (e.g. along elevational gradients or due to seasonal variations in temperature in temperate biomes). Along such spatial or temporal environmental gradients, one may observe gradual changes in the distribution of certain traits accompanied by changes in species' relative abundances or species turnover among communities (e.g. Cornwell and Ackerly 2009). In the end, it is the interaction of traits and the environment that affects species' performances. Environmental conditions may affect

the relationships of certain traits and the vital rates of individual organisms. The combination of all effects of individual traits on the vital rates then determines the relative fitness of the individual organism conditional on the environment it occurs in (Laughlin and Messier 2015).

At all levels of ecological organization processes involve probabilities, be it the probability of an individual caterpillar to be eaten by a bird before pupation or the probability of an island community to be extinguished by a volcanic eruption. The consequences of this random component may depend on the initial conditions, like for instance the initial number of individuals in a population (Vellend 2016). Additionally, processes driving dynamics on the organism, population or community level may take place on very different spatial and temporal scales (Levin 1992). The high level of contingencies and the interdependency of spatial and temporal scales impeded the development of reliable predictions concerning for instance the consequences of ongoing anthropogenic global change on populations and communities (Maris et al. 2018). Understanding trait-environment interactions and their role in determining vital rates and the probabilities for success of individuals, populations and communities considering spatial and temporal scales may however allow the generation of more reliable predictions in the future (Laughlin and Messier 2015, Laughlin et al. 2018). One promise of trait-based approaches is that the relationship of properties that are generalizable over organisms such as traits with similarly generalizable environmental conditions may lead to general trends that allow predictions for all levels of biological organization as well as for other geographical locations or predictions in the future (Shipley et al. 2006, Shipley 2007).

Aim of the thesis

This thesis aims at investigating how the environment and species' traits as well as their interaction affect community structure and dynamics on varying spatial and temporal scales. In order to derive predictions of how ecological communities will respond to ongoing environmental change in the future we need to understand (I) community responses to environmental gradients and their variation, (II) drivers of species' performances and (III) how species' traits affect species' success in a particular environment. Therefore, in this thesis I investigate patterns of alpha-, beta- and gamma-diversity along environmental gradients (chapter 2), factors driving species' performances in terms of distribution and abundance (chapter 3) and the effects of trait-environment interactions on community dynamics on small and large spatial scales (chapter 4).

Community structure along environmental gradients

In chapter 2, I present three studies that focus on the response of ecological communities in terrestrial forest ecosystems to environmental conditions changing along natural gradients. The first study explores the effect of change in climatic conditions along a local elevational gradient on the alpha-, beta- and gamma-diversity of 15 organism groups of plants, animals and fungi. For that matter I calculated generalized dissimilarity models to assess the rate of change in community dissimilarity due to species turnover or nestedness along the elevational gradient and performed an additive diversity partitioning to quantify the contribution of beta diversity among elevational zones to the overall gamma diversity of the region.

The second study applies a space-for-time approach in order to investigate species' responses in terms of abundance and richness, as well as community composition along the course of temperate forest succession from early establishment to decay. Here, we categorized forest stands into one of nine successional stages using remote sensing data and calculated generalized mixed linear models with polynomial contrasts for abundances and species numbers of forest dwelling organisms. Furthermore, we quantified the contribution of beta diversity among successional stages to the overall species pool by additive diversity partitioning. This study reveals varying responses of functional and taxonomic organism groups along the course of forest succession. Changes in environmental conditions associated with the different forest successional stages lead to high rates of species' replacement among forest sites and ultimately affect gamma-diversity of forests at a landscape scale.

While both aforementioned studies investigate the effects of climatic conditions and forest structural properties in a regional context the third study investigates these effects at a larger spatial scale, namely the distributional range of the European beech *Fagus sylvatica*. Here, the communities under study were arthropods inhabiting the tinder fungus *Fomes fomentarius*. The analysis of the community composition of 59 local communities aims at quantifying the relative importance of climate, space and forest structure at driving alpha and beta diversity in terms of species turnover and nestedness at a continental scale.

The role of species' traits in modulating species' success

In chapter 3, I present two studies that focus on species' performances in terms of local distribution and mean abundance in relation to species-specific traits. Both studies investigate the ubiquitous relationship of both performance measures - local distribution and mean abundance - by utilization of causal path modelling approaches. Here, the first study adopts generally proposed hypotheses formulated in order to explain this relationship and tests them in a combined framework. In order to explain the distribution-abundance relationship of phytophagous true bugs (Heteroptera) in managed grasslands, data on morphological and ecological traits associated with propensity for dispersal and resource utilization were compiled. All hypothesized relationships concerning the distribution-abundance relationship were formulated as structural equations according to the proposed underlying causality and tested separately as well as in a combined framework.

The second study further investigates the link between morphological traits and species' distributions and abundances, as the first study suggested no link between morphological traits and both measures of performance. Here, the resulting causal framework from the first study was extended by incorporating proxies for energy uptake and allocation strategies as a modulating factor between species' morphologies and performances. The assumptions of the resulting eco-physiological model were then tested using data on butterfly (Lepidoptera) populations from a monitoring program in Switzerland.

The role of trait-environment interactions for community dynamics across spatial scales

In chapter 4, I present two studies that investigate the covariation of species' traits and the environmental conditions the species occur in. Here, both studies focus on the selection for

thermoregulatory relevant functional traits by changing thermal conditions along spatial gradients. The first study implements a large-scale approach across Western Europe testing whether geometrid moth assemblages (Lepidoptera: Geometridae) exhibit a latitudinal decline in mean color lightness values, a trait assumed to affect insect thermoregulation. Thereby the study replicates the approaches of other studies on spatial patterns of color lightness (Zeuss et al. 2014, Pinkert et al. 2017) with the modification of including nocturnal insects that should not benefit as much of thermal melanism as diurnal insects.

If the assumptions of trait-based approaches in ecology hold true, we should detect the same pattern of trait-environment co-variation irrespective of the spatial scale or the taxon under study (Shipley et al. 2016). Therefore, the second study investigates the relationship between color lightness of geometrid moths and the thermal environment at a small spatial scale along a local elevational gradient. This study incorporates the closely related family of noctuid moths (Lepidoptera: Noctuidae) in the analysis. Furthermore, rather than indirectly assuming a trait-environment interaction based on the covariation of community weighted trait means and the thermal environment, this study directly tests the effect of the trait-environment interaction on species' performances.

The studies presented in the three chapters are either already published, under revision or in preparation for submission in peer-reviewed scientific journals. At the beginning of each chapter I briefly outline my contribution to the particular study. In each of the presented studies, the corresponding research questions and hypotheses are theoretically derived and presented with the necessary background information. Accordingly, all studies can be read independently of each other in any particular order.

Chapter 2.1

Biodiversity along an elevational gradient of the Bohemian Forest – the BIOKLIM project

with
Claus Bässler | Roland Brandl | Torben Hilmers | Jörg Müller | Linda Seifert

published in Silva Gabreta, 24 (1), 2018, p. 149 – 160

This article is part of a special issue in *Silva Gabreta* on the cooperative transboundary monitoring of the Bohemian Forest. The presented data is the result of extensive monitoring programs carried out in 2006 – 2009 mainly by Claus Bässler and Jörg Müller and repeated in 2016 by Torben Hilmers and me. During the fieldwork Mr. Hilmers conducted the monitoring of the forest structure and its attributes, while I conducted the biodiversity monitoring presented in this article. In our research Mr. Hilmers and I worked closely together resulting in this and two other joint publications (see chapter 2.2 and Hilmers et al. 2018a). The overall project and the transboundary cooperation were coordinated by Linda Seifert. This paper and the analyses therein are predominantly my personal contribution.

Summary

To monitor the response of forest biodiversity to environmental changes, the BIOKLIM project collected data on species occurrences along transects covering the elevational gradient within the Bavarian Forest National Park and adjacent areas. The monitoring program was launched in 2006 and repeated in 2016 as part of the Silva Gabreta Monitoring project. Here we show the potential of such regional monitoring programs for characterizing alpha, beta and gamma biodiversity of 15 groups of organisms along the elevational gradient in forests mainly dominated by European beech and Norway spruce. Overall, we recorded 4,179 species of which 1,918 are common (based on Shannon diversity) and 1,222 are dominant (based on Simpson diversity). Asymptotic extrapolation suggested that between 5,340 and 6,100 species might occur in the terrestrial ecosystems of the Bohemian Forest. Most groups showed significant responses in alpha diversity to elevation. However, the relationships varied strongly in strength and shape. Changes in species composition along the elevational gradient were mostly due to turnover and contributed strongly to the overall diversity of the study region. These first analyses show that monitoring schemes as implemented in the Silva Gabreta Monitoring offer the opportunity to study biodiversity along environmental gradients. In the long run resampling of the plots established in 2006 allows characterizing the responses of the communities to changes in forest structure and/or climate.

Introduction

Following a set-aside strategy, national parks aim at conserving ecosystems in a state as natural as possible and at protecting ecological processes that structure these systems (McNeely and Miller 1983). Nevertheless, national parks are not isolated and therefore biodiversity of the communities occurring within the protected area will change with time e.g. due to changes in the climate or disturbances (Hannah 2008). One important aim of national parks is therefore also to document such changes and to launch research to understand the processes that underpin fluctuations and trends of biodiversity (Heurich et al. 2010).

Founded in the year 1970, the Bavarian Forest National Park is the oldest national park in Germany. After its expansion in 1997 the national park covers an area of over 24,000 hectares and is part of the Bohemian Forest – the largest contiguous forest area in central Europe. After several consecutive disturbances, mostly due to wind throws and bark beetle outbreaks, the administration of the national park decided to implement a benign-neglect strategy and not to interfere (e.g. by salvage logging) with the natural processes (Müller et al. 2010). Thereby, deadwood availability and structural heterogeneity increased in large areas of the historically managed forest within the park (Lehnert et al. 2013). To monitor environmental changes within the park as well as the response of forest biodiversity to such natural disturbances, the BIOKLIM project was initiated in the year 2006 (Bässler et al. 2009). This project collected data on relevant environmental variables as well as data on the occurrence and abundance of species of plants, fungi and animals along the elevational gradient of the national park. These groups represent a large proportion of the diversity of central European forests. Such standardized surveys offer baseline data on the biodiversity that are necessary to assess the response of communities to changing environmental conditions and processes that structure these communities.

Furthermore, using a space-for-time approach the elevational gradient allowed first insights how the communities will change with global warming (Bässler et al. 2010b). As the Bavarian Forest National Park represents only a rather small proportion of the contiguous forest covering the Bohemian Massif, the BIOKLIM survey is now integrated in an interregional monitoring scheme conducted by the Bavarian Forest and Šumava National Parks as part of the Silva Gabreta Monitoring project (Křenová and Seifert 2015, 2018).

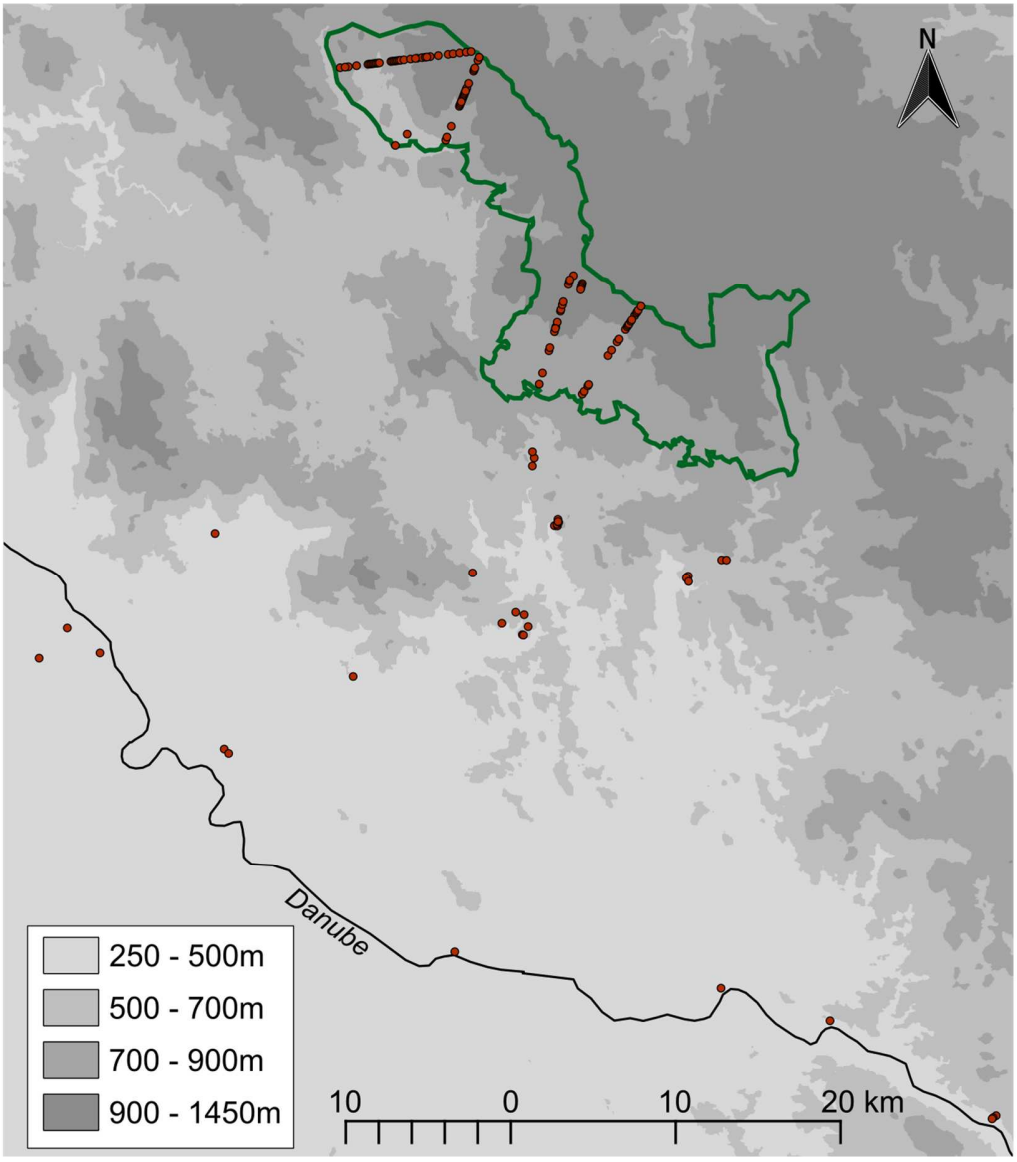

FIGURE 2.1.1. An overview map of the 133 sampling points (red points) across the elevational gradient. Main sampling transects are located within the Bavarian Forest National Park (green line). Additional lowland plots (<650 m a.s.l.) outside the NP extended the elevation gradient down to the Danube River representing the gradient from 287–1420 m a.s.l. Some sampling points are not visible (overlaid) due to scaling.

As part of this monitoring scheme, the survey of the biodiversity inhabiting the forests along the elevational gradient was repeated in the year 2016 (Bässler et al. 2015) and additionally this monitoring was expanded to streams (Bojková et al. 2018).

To show the potential of repeated surveys as implemented here, we present data on the diversity of 15 groups of organisms based on the two surveys conducted in the years 2006 and 2016. The aim of this study is to give a general overview of the biodiversity found in the Bavarian Forest National Park and adjacent areas (gamma diversity) and how biodiversity in terms of alpha and beta diversity is structured along the elevational gradient in the terrestrial ecosystems of the Bohemian Forest. Here, our analyses are based on a harmonized dataset from the two surveys in 2006 and 2016 generated with similar sampling methods conducted on the same study plots.

Methods

Sampling area

The surveys were conducted in 2006 and repeated in 2016 in the German part of the Bohemian Forest covering an elevational gradient from 287 to 1420 m a.s.l. Details of these two surveys are described in Bässler et al. (2009, 2015). The original design of 331 study plots was optimized for resampling in 2016 in order to cover the structural gradient across the whole elevational gradient and to maximize the number of plots covered by both surveys (Bässler et al. 2015). The final set of plots with harmonized data of both surveys used in this study consisted of 133 plots ranging from plots at low elevations in the Danube valley to high elevation plots on the mountain ranges of the Bavarian Forest National Park (Fig. 2.1.1).

TABLE 2.1.1. Sampling methods for the groups sampled during the BIOKLIM project. FC – field collection, PT – pitfall traps, FIT – flight-interception trap, MT – malaise trap, LT – light trap. Number of species refers to the overall number of species found on the plots during both surveys. Number of plots refers to the number of plots with harmonized data for both survey years.

Group	Taxon	FC	PT	FIT	MT	LT	Number of species	Number of plots
Plants	Spermatophyta	x					297	133
Soil mosses	Bryophyta	x					84	109
Wood mosses	Bryophyta	x					149	109
Lichens	Fungi	x					125	109
Fungi	Fungi	x					562	133
Snails and Slugs	Gastropoda	x					103	133
Birds	Aves	x					51	133
Bees and wasps	Aculeata				x		308	52
Beetles	Coleoptera		x	x			1305	132
Cicadas	Cicadoidea				x		215	52
Hoverflies	Syrphidae				x		185	52
Moths	Lepidoptera					x	272	33
Spiders	Arachnida		x	x			292	132
Springtails	Collembola		x				51	132
True bugs	Heteroptera			x	x		180	52
Sum							4179	

Species Sampling

Species sampling of both surveys followed the same methods for each taxonomic group on the 133 study plots. Overall 15 groups of plants, fungi, and animals were included in this study (Table 2.1.1). The taxonomic rank differed considerably (Table 2.1.1). Species were sampled using standard methods suitable for an appropriate sampling of the respective taxon. Higher plants, fungi, and birds were recorded on all 133 plots. Insect samples from flight-interception and pitfall traps of one plot were unfortunately lost in 2016. The other taxa were sampled on subsets of the study plots due to the constraints imposed by labor-intensive collection methods. We applied hand collections (gastropods, number of the study plots surveyed: n = 108), field mapping (lichens, wood mosses and soil mosses, n = 109), flight-interception traps (beetles, true bugs, spiders and harvestmen, n = 132), pitfall traps (beetles, springtails, spiders and harvestmen, n = 132), malaise traps (bees and wasps, cicadas, hoverflies and true bugs, n = 52) and light traps (moths, n = 33; Table 2.1.1). For details of the sampling methods used for different taxa, see Bässler et al. (2009, 2015). All specimens were determined to species by specialists for the respective taxon. For the present communication, the occurrence data of both surveys were aggregated in presence-absence matrices. Thus, the results of the present analysis do not distinguish between the two sampling events.

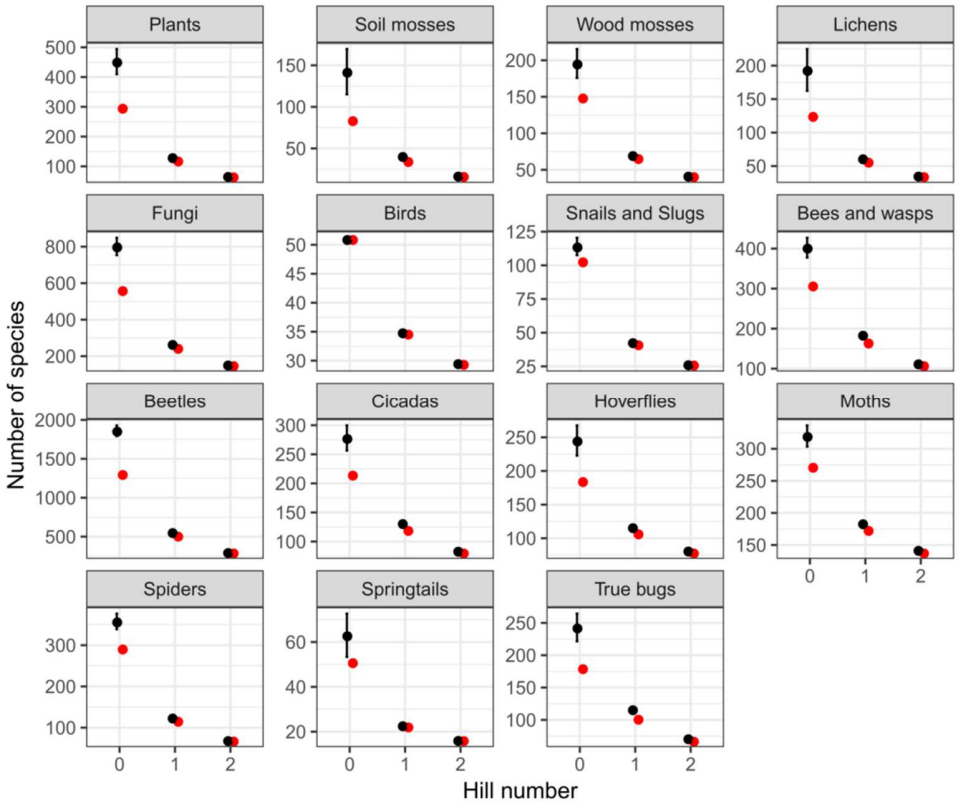

FIGURE 2.1.2. Observed as well as asymptotic estimates of the number of species of 15 important taxonomic groups. Calculations are based on Hill numbers of the orders 0 (i.e. species richness), 1 (i.e. Shannon diversity representing 'common' species), and 2 (i.e. Simpson diversity representing 'dominant' species). Black circles indicate asymptotic estimations with standard errors. Red circles indicate observed values.

Table 2.1.2. Results of the generalized linear models of the number of species of the 15 studied groups. Elevation was included as a linear and quadratic predictor to account for nonlinear relationships. Tables show z-values of the predictor together with its statistical significance and the explained deviance of the model. Groups with significant effects of elevation on the number of species are given in bold.

Group	Elevation (z-value)	*P*-value	Elevation^2 (z-value)	*P*-value	Explained deviance
Plants	**−6.55**	**<0.001**	**5.53**	**<0.001**	**0.08**
Soil mosses	1.58	0.114	−1.90	0.057	0.03
Wood mosses	**3.51**	**<0.001**	**−3.54**	**<0.001**	**0.04**
Lichens	1.52	0.133	0.17	0.866	0.28
Fungi	**3.05**	**<0.050**	**−4.62**	**<0.001**	**0.20**
Birds	0.10	0.918	−0.68	0.494	0.12
Snails and Slugs	**−4.67**	**<0.001**	**1.96**	**<0.050**	**0.43**
Bees and wasps	**−8.10**	**<0.001**	**3.11**	**<0.050**	**0.58**
Beetles	**−9.65**	**<0.001**	**8.28**	**<0.001**	**0.15**
Cicadas	**−7.77**	**<0.001**	**6.56**	**<0.001**	**0.27**
Hoverflies	−0.09	0.928	−0.23	0.817	0.01
Moths	**2.12**	**<0.050**	**−2.61**	**<0.05**	**0.13**
Spiders	**−6.99**	**<0.001**	**7.93**	**<0.001**	**0.29**
Springtails	−0.44	0.661	0.78	0.437	0.07
True bugs	**−5.15**	**<0.001**	**4.49**	**<0.001**	**0.21**

Analysis

All statistical analyses were conducted in the software environment R (v. 3.4.3; R Core Team 2017). To estimate metrics of species richness, we used the rarefaction-extrapolation framework suggested by Chao et al. (2014) using the aggregated matrices. We calculated Hill numbers for the aggregated matrices to analyze the diversity of common and dominant species within one framework. Hill numbers represent a family of diversity indices expressed in effective numbers of species that differ among themselves by the exponent q (Hill 1973, Chao et al. 2014). The value of q determines the sensitivity of the diversity measure to rare or common species. Here, Hill numbers with q = 0 are equivalent to the species richness of the assemblage which counts species without regard to their prevalence. Hill numbers of orders lower than 1 are sensitive to rare species, while orders higher than 1 are sensitive to the most common or dominant species (Jost 2007). Hill numbers with q = 1 conform to the exponential of the frequently used Shannon index and represent the effective number of common species. Hill numbers with q = 2 are termed Simpson diversity and discount all but the most common or dominant species (Hsieh et al. 2016).

In order to get comparable estimates based on sampling effort we rarified respectively extrapolated the diversity estimates for all groups to 99 sites, which leads to an extrapolation by a factor of three for the group sampled on the fewest number of sites (moths sampled on 33 sites; Hsieh et al. 2016). Additionally, we calculated estimates of the asymptotic richness (i.e. the number of species after extrapolation to the point where an increase in sampling units does not further increase the number of species) for each group separately as an estimate of the lower bound of total species richness as well as the number of common and dominant species (Chao 1987). We used 999 replicated bootstraps to calculate confidence intervals around the species-accumulation curves. These methods are implemented in the iNEXT package (Hsieh et al. 2016).

In order to investigate the response of each of the 15 taxa to the elevational gradient on alpha diversity we modeled the number of observed species for each site using generalized linear models with a Poisson error distribution with

elevation above sea level as linear and quadratic predictor. For the analysis of beta diversity, we calculated pairwise Sørensen dissimilarity indices across the assemblages of all 15 groups, based on species-site matrices with varying dimensions depending on the respective group. Beta diversity was partitioned into its additive components of turnover (i.e. dissimilarity due to replacement of species) and nestedness (i.e. dissimilarity due to species loss; Baselga 2010). Subsequently, we calculated generalized dissimilarity models (GDM) on distance matrices for both the turnover and nestedness component including elevation above sea level as predictor variable, while controlling for spatial distance by including the spatial position of the site into the model (i.e. GPS coordinates). GDMs allow the analysis of spatial patterns of community composition under consideration of non-linear relationships between dissimilarity in community composition along environmental gradients (Ferrier et al. 2007). All GDMs were calculated using the default of three I-splines. The calculated coefficient for each of the three I-splines represents the rate of change along a third of the gradient of the environmental predictor when keeping all other predictors constant (i.e. high values of the first I-spline indicate a high rate of change along the first third of the gradient). To quantify the contribution of alpha and beta diversity among plots and among elevational zones to the overall gamma diversity in our study system, we used additive diversity partitioning as implemented in the R package vegan, version 2.4-6 (Oksanen et al. 2018).

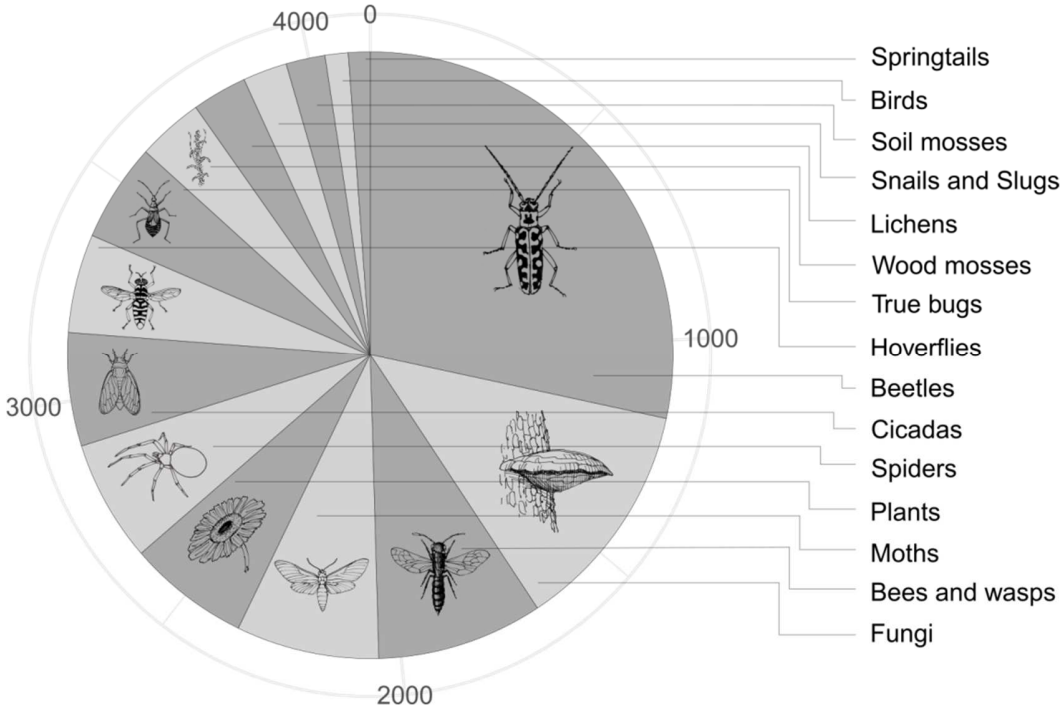

FIGURE 2.1.3. Relative proportions of the species richness of the 15 groups under study after rarefaction/interpolation on three times the sampling units of the taxonomic group with the lowest number of sampling sites (i.e. 3 × 33 sites = 99 sites). Segment sizes conform to the number of species of the organism group with an overall estimated number of 4135 species.

For this analysis, we divided the elevational gradient into five equally spaced zones (1: 287–514 m a.s.l., n = 22; 2: 514–740 m, n = 33; 3: 740–967 m, n = 32; 4: 967–1193 m, n = 37; 5: 1193–1420 m, n = 33). The levels of the sampling hierarchy thus included the alpha diversity at the plot level, beta diversity among plots, beta diversity among elevational zones, and the overall gamma diversity.

Results and Discussion

Based on the data from both surveys, we recorded 4,179 species of which 1,918 are common (Shannon diversity) and 1,222 are dominant (Simpson diversity). The mean number of species per site and across all sampled taxa was 417±21 species (mean ± standard error). Overall, the sampling effort of our surveys was sufficient to cover most of the common and dominant species of the study system and an increase in sampling effort would only increase the number of rare species for some groups as indicated by the differences between estimated and observed number of species for the three orders of Hill numbers (Fig. 2.1.2): For order 0 which includes also rare species the difference is rather large compared to the other two orders. Beetles and fungi account for more than a quarter of all species and contribute considerably to the overall (gamma) biodiversity (Fig. 2.1.3). After asymptotic extrapolation, the expected species richness ranges from 5,340 to 6,100 species for the terrestrial ecosystem of the national park. However, our methods were not able to generate reliable data for the species living in the canopy (especially phytophagous insects), soil or deadwood dwelling species. Thus, the estimate of 6,100 species is only a lower bound for the total terrestrial biodiversity. Furthermore, this study ignored aquatic ecosystems like rivers or bogs, which also host species rich communities and have been the subject of an additional survey as part of the Silva Gabreta Monitoring project (Bojková et al. 2015, 2018, Křenová and Seifert 2015). Our results show that the elevational gradient forms one of the major gradients of environmental change for biotic communities in the Bohemian Forest. Besides changes in macroclimatic conditions, the elevational gradient is accompanied by several changes in forest types and structures. Our lower sites in the Danube valley range from riparian forests at the most western sites in the river delta of the Isar and the Danube River to a xerothermic forest at the steep southern slope of the Jochensteiner Hänge near Passau. As typical for low mountain ranges in Europe, the higher sites are covered by mountain mixed forests with European beech (*Fagus sylvatica*) as the dominant species at mid elevations and Norway spruce (*Picea abies*) at high elevations (Heurich and Neufanger 2005, Barbati et al. 2014, Hilmers et al. 2018b). Thus, it is not surprising that the observed number of species also change with elevation as found for nearly all taxa in our study. However, patterns of these changes vary strongly in strength and shape ranging from more or less linear declines to more complex U- and hump-shaped relationships (Fig. 2.1.4, Table 2.1.2). In general, changes in community composition along the elevational gradient are mostly due to species turnover among sites. Nestedness showed no obvious pattern with elevation: i.e. nestedness of the communities does not increase with elevation (Fig. 2.1.5, Table 2.1.3). Thus, we do not observe increased rates of species loss as we would expect if environmental conditions get harsher or too harsh for most species at higher elevations. The constant turnover of species along the elevational gradient contributes strongly to the observed gamma diversity of the Bohemian Forest. Additive partitioning showed that for most taxa beta diversity among

elevational zones contributed most to the overall observed species pool, exceeding the contributions of local alpha diversity and beta diversity among plots within elevational zones (Fig. 2.1.6).

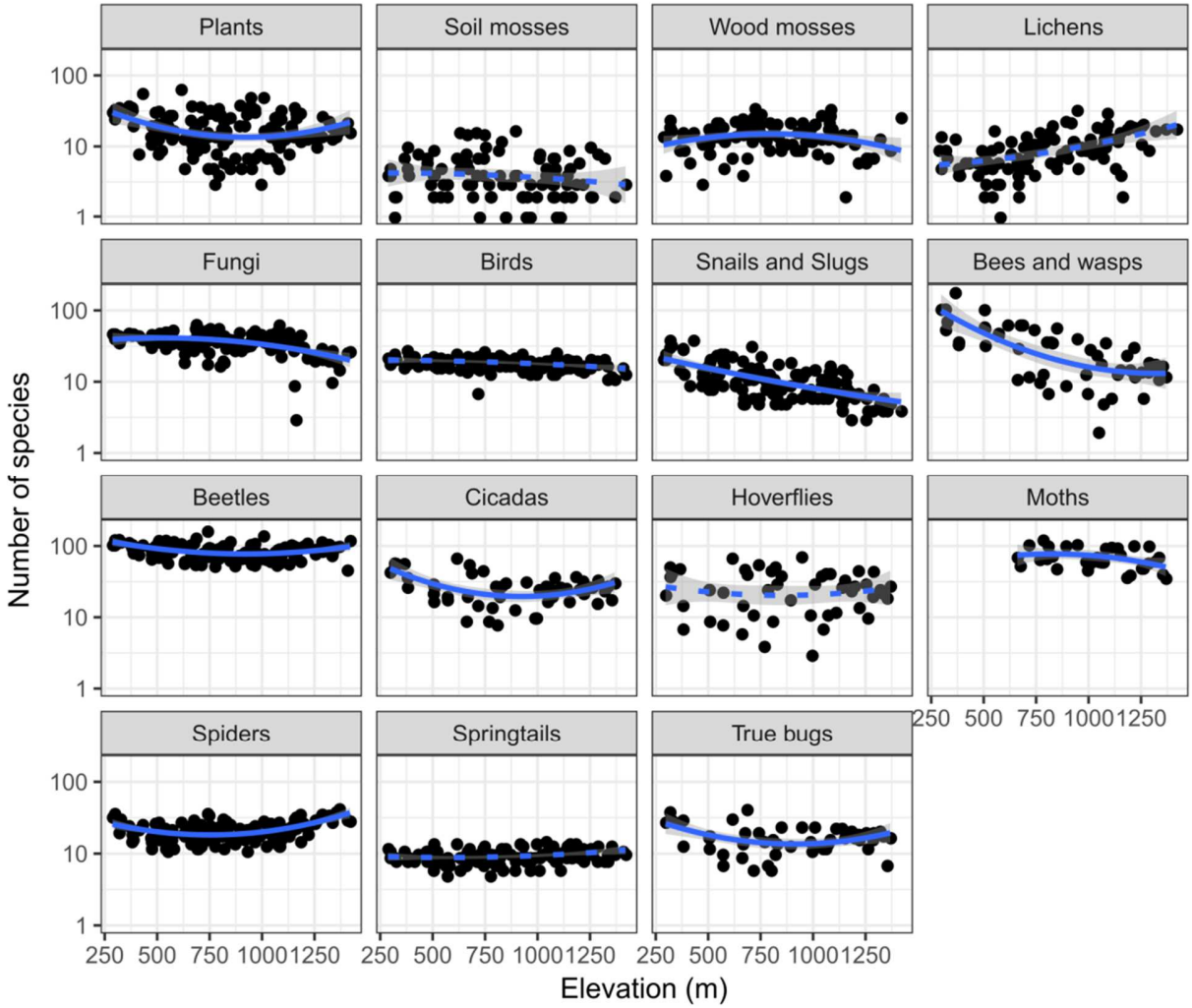

FIGURE 2.1.4. Relationships of the number of species with elevation above sea level for the 15 groups of sampled organisms. Each point represents the number of species observed at a study site during the two surveys. Blue lines are based on generalized linear models with elevation as linear and quadratic predictor. Shaded areas indicate 95 % confidence intervals. Dashed lines indicate no significant effect of elevation on the number of species.

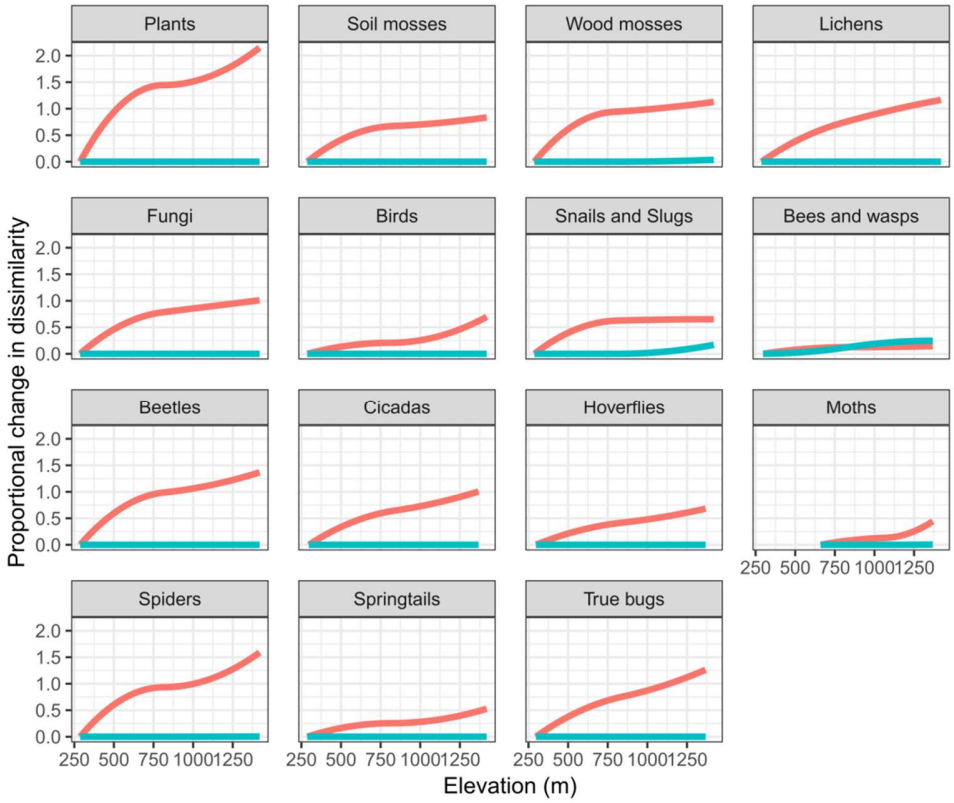

FIGURE 2.1.5. I-Splines of generalized dissimilarity models after beta diversity partitioning into its turnover and nestedness components. For each group two models were calculated with dissimilarities among sites partitioned in turnover and nestedness as response matrices and dissimilarity among sites in geographic space (i.e. latitude and longitude) and elevation a.s.l. as predictor matrices. Red lines indicate the rate of change in dissimilarity due to turnover along the elevational gradient. Blue lines indicate the rate of change in dissimilarity due to nestedness along the elevational gradient.

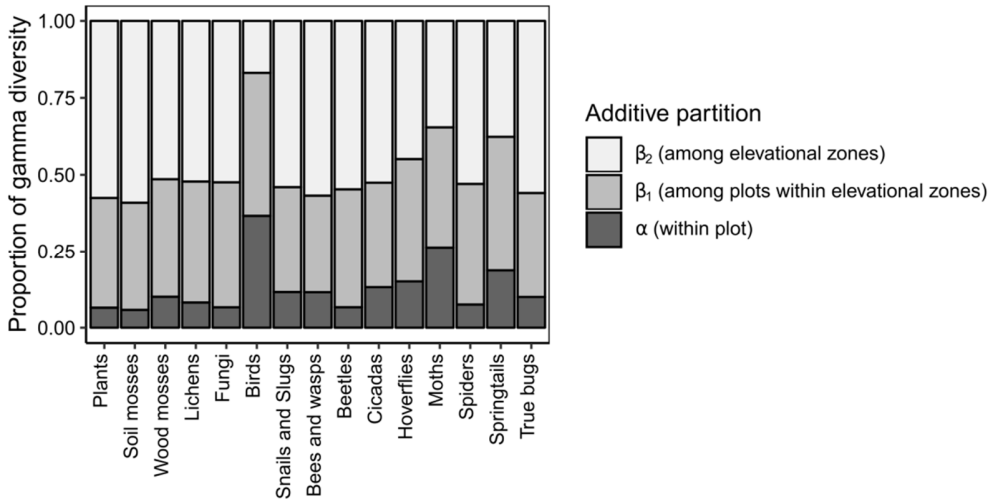

FIGURE 2.1.6. Results of additive partitioning with three levels of sampling hierarchy including plot-level diversity (i.e. α-diversity), β-diversity among plots within five equally spaced elevational zones, as well as β-diversity among elevational zones. The height of the stacked bar indicates the relative contribution of the respective level of sampling hierarchy to the overall observed diversity (i.e. gamma diversity).

TABLE 2.1.3. Percentage of explained deviance of the generalized dissimilarity models by dissimilarity in elevation a.s.l. as a predictor for community dissimilarity in terms of turnover or nestedness.

Group	Explained deviance	
	Turnover	Nestedness
Plants	35.8	0
Soil mosses	5.5	0
Wood mosses	24.7	0.3
Lichens	12.5	0
Fungi	20.7	0
Birds	35.8	0
Snails and Slugs	21.9	4.2
Bees and wasps	1.7	5.6
Beetles	46.6	0
Cicadas	41.1	0
Hoverflies	15.1	0
Moths	25.6	0
Spiders	33.3	0
Springtails	13.6	0
True bugs	26.3	0

Conclusions

The implementation of the monitoring scheme generated reliable data for all taxonomic groups under study. This enables upcoming studies to investigate changes in species richness and community composition as well as changes in the elevational distribution of species in response to a changing climate and changes in forest structure (Bodin et al. 2013). Here, a first study of Hilmers et al. (2018b) revealed differential responses of taxonomic and trophic groups to stages of forest succession in the study region, which offers a dynamic baseline for assessing the effects of external drivers such as changes in the temperature regime (Bodin et al. 2013, Thom et al. 2017). To overcome the shortcomings of a space-for-time approach it is necessary to resample the elevational gradient in regular intervals (Bässler et al. 2015). Although urgently needed, long-term regional biodiversity surveys along environmental gradients accompanied by a monitoring of changes in environmental conditions and habitat variables are still rare in ecological research (Lepetz et al. 2009; but see Greenland et al. 2003). Several studies revealed that species might respond to ongoing environmental change by adapting their distributions, including elevational upward shifts due to increasing temperatures (Bässler et al. 2013, Rumpf et al. 2018). Here, species' responses might vary strongly in strength and even direction (Lenoir et al. 2010, Bässler et al. 2013, Alexander et al. 2018). Despite their static nature, protected areas have the potential to buffer negative impacts of climate change on species by improving habitat quality and quantity (Thomas and Gillingham 2015, Betts et al. 2017). Thus, for the successful implementation of conservation measures it is crucial to understand how species will respond to changing environmental conditions and which species are most threatened. The BIO-KLIM project and its continuation as part of the Silva Gabreta Monitoring will make an important contribution in the endeavor to understand species' responses to global change.

Acknowledgments

This research was supported by the Bavarian State Forestry and the Bavarian State Ministry of the Environment, Public Health, and Consumer Protection. Monitoring activities from 2016 to 2018 and publishing was granted by the transboundary cooperation program Bavaria Free State–Czech Republic–ETC goal 2014–2020, the Interreg V project No. 26 "SILVA GABRETA Monitoring: Realization of a transboundary Monitoring of Biodiversity and Water Balance". Additionally, TH and NF received scholarships from the Rudolf and Helene Glaser Foundation organized in the "Stifterverband für die deutsche Wissenschaft". We thank two anonymous referees for valuable comments on the initial submission.

Chapter 2.2

Biodiversity along temperate forest succession

with

Torben Hilmers | Claus Bässler | Marco Heurich | Roland Brandl | Hans Pretzsch | Rupert Seidl | Jörg Müller |

published in Journal of Applied Ecology, 55 (6), 2018, p. 2756– 2766

This paper is mainly the result of the close cooperation of Torben Hilmers (lead author) and me (corresponding author). Here, we contributed equally to the conceptual design of the study, the data analysis and the writing of the manuscript. With substantial input from all our co-authors and supervised by Marco Heurich, Hans Pretzsch, Roland Brandl and Jörg Müller this paper is predominantly the shared contribution of Mr. Hilmers and me. For this chapter, there is a digital supplement with additional data on the enclosed compact disk.

Summary

The successional dynamics of forests – from canopy openings to regeneration, maturation and decay – influence the amount and heterogeneity of resources available for forest-dwelling organisms. Conservation has largely focused only on selected stages of forest succession (e.g. late-seral stages). However, to develop comprehensive conservation strategies and to understand the impact of forest management on biodiversity, a quantitative understanding of how different trophic groups vary over the course of succession is needed. We classified mixed mountain forests in Central Europe into nine successional stages using airborne LiDAR. We analyzed α- and β-diversity of six trophic groups encompassing approximately 3,000 species from three kingdoms. We quantified the effect of successional stage on the number of species with and without controlling for species abundances and tested whether the data fit the more-individuals hypothesis or the habitat heterogeneity hypothesis. Furthermore, we analyzed the similarity of assemblages along successional development. The abundance of producers, first-order consumers and saprotrophic species showed a U-shaped response to forest succession. The number of species of producer and consumer groups generally followed this U-shaped pattern. In contrast to our expectation, the number of saprotrophic species did not change along succession. When we controlled for the effect of abundance, the number of producer and saproxylic beetle species increased linearly with forest succession, whereas the U-shaped response of the number of consumer species persisted. The analysis of assemblages indicated a large contribution of succession-mediated β-diversity to regional γ-diversity. Depending on the species group, our data supported both the more-individuals hypothesis and the habitat heterogeneity hypothesis. Our results highlight the strong influence of forest succession on biodiversity and underline the importance of controlling for successional dynamics when assessing biodiversity change in response to external drivers such as climate change. The successional stages with highest diversity (early and late successional stages) are currently strongly underrepresented in the forests of Central Europe. We thus recommend that conservation strategies aim at a more balanced representation of all successional stages.

Introduction

After a severe disturbance with high tree mortality, forests undergo a series of successional stages. Following successful regeneration, forests canopies eventually close and subsequently diversify in both their vertical and horizontal structures. With ongoing succession, forests accumulate biomass, and the initial cohort of trees gradually dies, which increases the amount of dead wood (Oliver and Larson 1990, Franklin et al. 2002). Recent studies have revealed a dynamic and increasingly complex picture of forest succession that suggests the possibility of multiple successional pathways and nonlinear effects of varying disturbance severities (Donato et al. 2012, Tepley et al. 2013). Nevertheless, key attributes of forests, such as carbon storage and biodiversity, are inherently linked to their successional stages (Seidl et al. 2016).

Despite the fundamentally dynamic nature of forests, accounting for successional dynamics remains a challenge for the development of conservation concepts (Tikkanen et al. 2007). Based on a limited number of focal species and their habitat preferences, conservation efforts often focus on one or a few successional stages (Swanson et al. 2011).

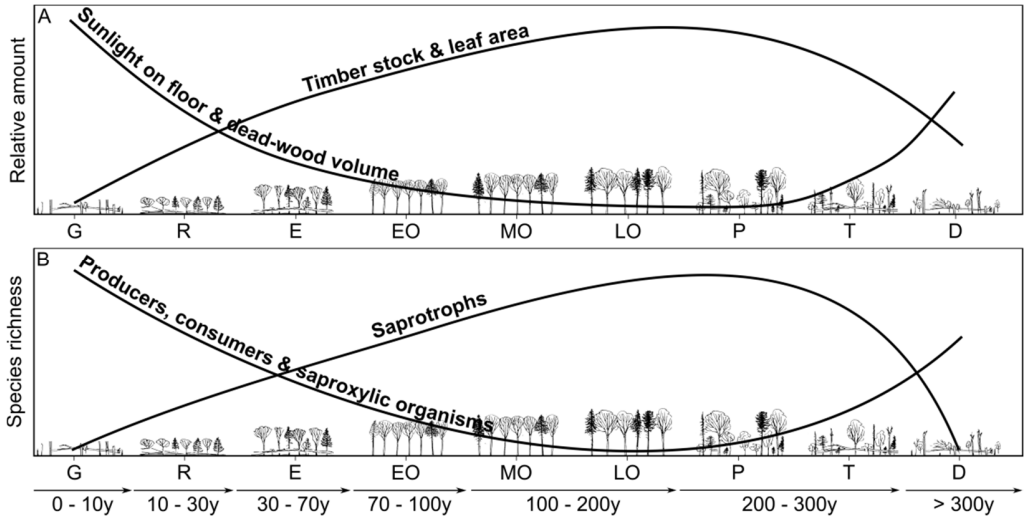

FIGURE 2.2.1. (A) Changes in resource availability with forest succession and (B) hypothesized response of saprotrophs, saproxylic organisms, producers and consumers. The successional stages considered here follow Tabaku (2000), Drössler & Meyer (2006) and Zenner et al. (2016). Arrows represent an approximate timeline of the successional stages following Moning & Müller (2009). Note that the decay stage can occur already after 120 years due to forest disturbances, such as storms and bark beetle infestations. Stages: G, gap; R, regeneration; E, establishment; EO, early optimum; MO, mid optimum; LO, late optimum; P, plenter; T, terminal; D, decay.

For instance, it has been shown that late stages of forest succession, including plenter (mixture of trees of different ages, sizes and heights), terminal and decay stages, are the preferred habitat for species considered as typical "forest dwellers", e.g. white-backed woodpecker in Central Europe (*Dendrocopus leucotos*; Carlson, 2000). Late successional stages are often prioritized in conservation due to their high diversity in taxa, including birds, bats, saproxylic organisms (Jacobs et al. 2007, Avila-Cabadilla et al. 2009, Peña-Cuéllar et al. 2012), lichen (Kuusinen and Siitonen 1998) and fungi (Redecker et al. 2001).

Understanding the inherent changes in species diversity as forests develop provides an important baseline for assessing the effects of external drivers such as climate change (Thom et al. 2017). In the absence of such a dynamic baseline, observed changes in biodiversity that are simply the effect of forest dynamics could be easily misattributed to effects of climate change. Furthermore, understanding the variation in biodiversity over the entire course of succession could also provide a more comprehensive perspective on the effects of different management strategies on biodiversity. In Europe, for instance, the majority of forests are currently of intermediate age, as a result of heavy exploitation during and after the first half of the 20th century (Vilén et al. 2012). Late stages of forest succession, such as the terminal and decay stages, are largely absent; as most forests are harvested before trees reach old age (Faustmann 1995). Similarly, early successional stages are kept as short as possible by planting trees (Parker et al. 2000) or employing silvicultural techniques that accelerate stand development (Dale et al. 2001).

Variation in biodiversity along the stages of succession can also help to better understand the underlying drivers of diversity in forests. For instance, resources that are relevant for different species groups, such as light on the forest floor and dead wood, distinctly vary with successional stage. The more-individuals hypothesis – a variant of the species-energy hypothesis (Wright 1983) – suggests that an

increase in resource availability leads to more individuals (Hurlbert 2004). In individual-rich communities, more species reach viable population sizes, which increase the observed number of species. Another factor is the diversity of resources (Cramer and Willig 2005). If particular stages of forest succession offer more resource types than others, these stages could harbor a larger number of species. This variant of the habitat heterogeneity hypothesis predicts an increase in the number of species independent of abundance (MacArthur and MacArthur 1961).

To assess changes in α- and β-biodiversity over forest succession, we quantified the abundance and diversity of 23 taxonomic lineages representing 6 trophic groups across 9 successional stages of forest succession (Fig. 2.21A). Based on theoretical considerations and the expected changes in the amount and heterogeneity of resources along the stages of succession (Fig. 2.2.1A), we hypothesized that:

(H1) patterns of abundance and number of species of primary producers along the course of forest succession would be U-shaped, dependent on light reaching the forest floor; patterns of consumers would be U-shaped, if they depend on the primary producers; patterns of saproxylic organisms would be U-shaped, if they are dependent on the accumulation of dead wood along succession; and patterns of saprotrophs would be hump-shaped, following the pattern of biomass accumulation;

(H2) the stage of forest succession would have no effect on the number of species when abundance is accounted for, if these responses are driven by an increase in individuals, as predicted by the more-individual hypothesis; and

(H3) species compositions in the early and late successional stages, which are characterized by open canopies, would be similar as many insects respond to the openness of the habitat.

Methods

Study area

We used data from a survey of biodiversity and forest structure in the Bavarian Forest National Park in south-eastern Germany (Bässler et al. 2009). The study area covers 24,000 ha and comprises a wide range of stages of forest succession that resulted from considerable variation in disturbance history and stand age. We utilize this variation in a space-for-time substitution approach in our analysis. The total annual precipitation is between 1300 and 1900 mm and increases with elevation (Fig. 7.1.1A), which ranges from 655 to 1420 m a.s.l. Annual mean air temperature varies between 3.5 °C at high elevations and 7.0 °C at low elevations (Bässler 2004). The national park is dominated by mixed mountain forests of Norway spruce (*Picea abies* (L.) Karst.), silver fir (*Abies alba* Mill.) and European beech (*Fagus sylvatica* L.).

Data

Forest structure was characterized from field measurements and airborne light detection and ranging (LiDAR) on 287 plots, each with a circular area of 1000 m². The plots include stands that were managed until a few decades ago and also remnants of old-growth forests. All measurements were conducted in the years 2006–2008 (Bässler et al. 2009). For each study plot, GPS coordinates were used to extract information on elevation from a digital terrain model (DTM 25) of the national park.

In a space-for-time substitution approach, differences in the environmental conditions of

sites often bias the analysis. Therefore, we collected data on both soil characteristics and macro-climate for each plot (for details, see chapter 7.1). By using elevation and the first PCA axis of soil parameter, we were able to control for potential differences.

The vegetation in the herbaceous layer (up to 1 m height), shrub layer (up to 5 m height), tree layer 1 (>5 to 15 m height) and tree layer 2 (>15 m) were estimated on 200 m² circular plots. Standing and downed woody debris were recorded in the field on each plot. Full-waveform LiDAR data were collected across our plots using a Riegl LMS-Q560 under leaf-on conditions in 2007 (nominal sensor altitude: 400 m, average point density: 25 points m^{-2}). Single trees in an area of 1000 m² around the center of each plot were detected using 3D segmentation (for details, see chapter 7.1).

Stages of forest succession

In our study, plots were classified to successional stages by combining the decision trees of Zenner et al. (2016) and Tabaku (2000; Fig. 7.1.2). These decision trees incorporate information on canopy projection area, maximum diameter at breast height (DBH), proportion of dead wood, normalized quartile of the DBH, and the cover and height of the regeneration layer (Fig. 7.1.2). The combination of these two protocols was necessary as Zenner et al. (2016) only considered trees with DBH >7 cm, and Tabaku (2000) explicitly also included regeneration and establishment stages. The combined decision tree was used to identify nine successional stages on 287 plots, i.e., gap, regeneration, establishment, early-optimum, mid-optimum, late-optimum, plenter, terminal and decay stages (Fig. 2.2.1).

Taxonomic groups

We analyzed the variation in biodiversity with forest succession considering 2956 species from 23 taxonomic lineages. The species were group-specifically sampled in a standardized way and covered six trophic groups: producers (higher plants, lichen, mosses), consumers I (phytophagous and pollinating arthropods), consumers II (invertebrates feeding on animal tissue), consumers III (vertebrates feeding on animal tissue), saprotrophs sensu lato (species feeding on dead tissue), and the special case of saproxylic saprotrophs (species depending on dead wood during their life cycle). Overall, this distinction of the 23 lineages into trophic groups yielded 33 functional groups; each of these functional groups was analyzed on 29–287 plots (for details, see chapter 7.1, Table 7.1.1).

Statistical analysis

All analyses were conducted in R (v. 3.3.2; R Core Team 2016). To test the influence of successional stage on the diversity of the 33 functional groups in the 6 trophic levels (Table 7.1.1) we calculated generalized linear mixed models with a Poisson distribution. We modelled either the number of species sampled on each plot (Gotelli and Colwell 2001) or abundances (i.e. the number of all sampled individuals of a taxon) as response variables, with successional stage as the predictor. To test for regular trends across successional stages using linear and quadratic contrasts, we coded the factor forest successional stage as ordered. Elevation and soil characteristics were included as additional predictor to control for confounding effects of the local conditions. To account for the overdispersion frequently observed in models of count data, we included an observation-level random effect (i.e. the plot) in all models (Harrison 2014). First, we calculated the overall effect (U- or hump-shaped response) of the

forest successional stage modelled with linear and quadratic contrasts on the number of species or abundances of all 33 functional groups. We tested whether differences in the number of species are in accordance with the predictions of the more-individuals hypothesis or the habitat heterogeneity hypothesis by controlling for abundances in a subsequent model using the number of species as response variable, while accounting for abundances (note that with the exception of plants, all abundance values were square-root transformed). Second, we used the models to predict the number of species in each group while keeping elevation and soil parameters constant. Since forest successional stages do not always proceed in an orderly manner in reality (e.g. due to storms or bark beetle infestation), the successional stage was incorporated as an unordered factor in this case. Predictors were tested for significance using a general linear hypothesis testing framework as implemented in the multcomp R package version 1.4-6 (Hothorn et al. 2016).

At the community level, we calculated multiple-site dissimilarities for taxonomic groups using the Sørensen dissimilarity index and partitioned the thus derived β-diversity into its additive turnover and nestedness components as implemented in the betapart R package version 1.4-1 (Baselga et al. 2017). To quantify the contribution of β-diversity among plots and among stages of forest succession to the γ-diversity in our study system, we used additive diversity partitioning as implemented in the R package vegan, version 2.4-3 (Oksanen et al. 2017). For a statistical test of the potential effects of forest succession on assemblages, we performed multivariate analyses of variance using distance matrices based on presence–absence data, applying the adonis function with 999 permutations as implemented in the vegan package. These analyses considered taxonomic groups with sufficiently high numbers of species not separated into trophic levels (i.e. excluding taxonomic groups with $\leq$ 30 species). Changes in species composition of these taxa along forest succession were illustrated using partial correspondence analyses (CA) conditioned on the effects of elevation and soil. Furthermore, we calculated the number of unique species for early (gap, regeneration and establishment), mid (early, mid and late optimum) and late (plenter, terminal and decay) stages of forest succession to evaluate the importance of individual stages for certain species of the taxa under study. In this case, we resampled a fixed number of plots in the early, mid and late stages, respectively, for each taxon in our study and calculated the number of species unique to these forest successional stages. The fixed number of plots was defined as half the number of plots of the rarest stage for each taxon. The resampling procedure was randomly repeated 1000 times, and the mean number of unique species per forest succession phase was calculated.

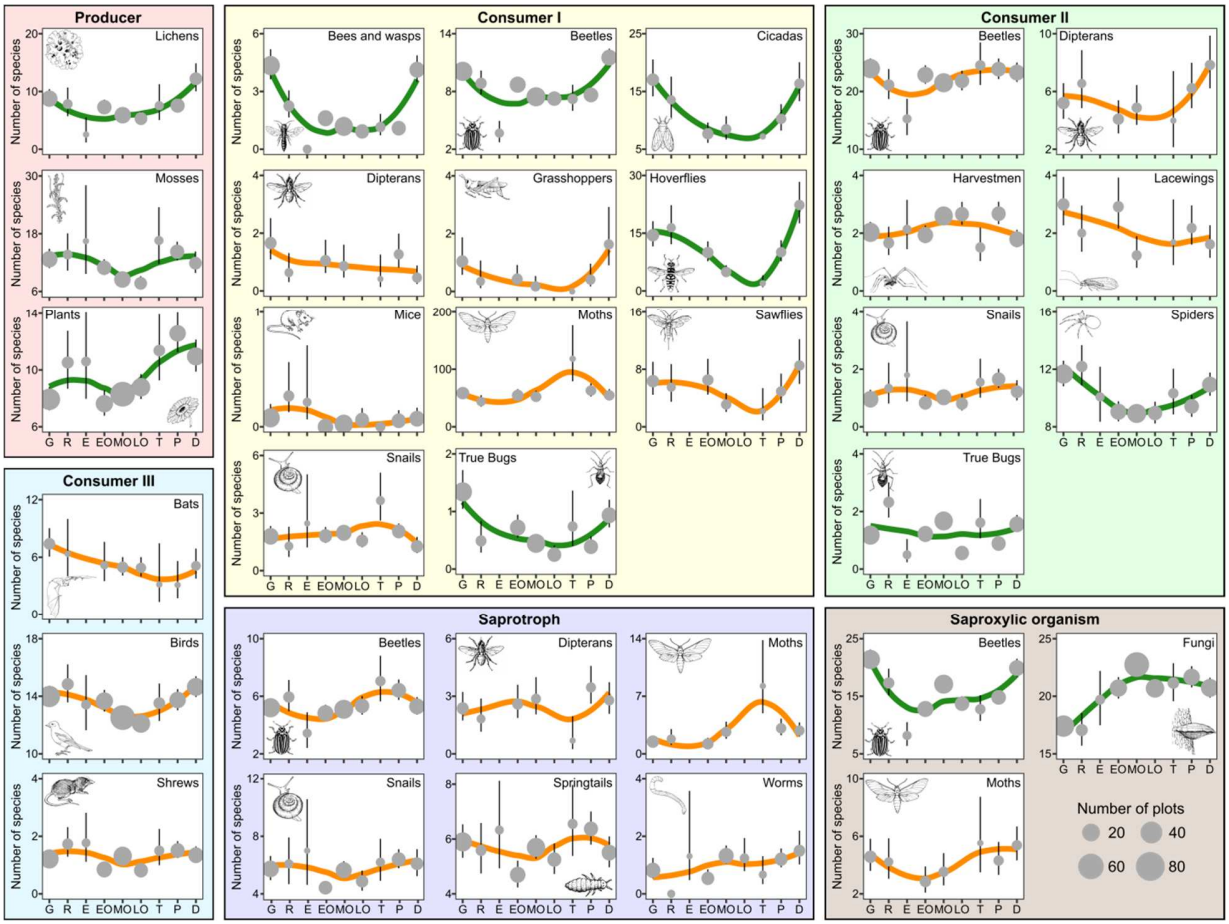

FIGURE 2.2.2. Variation in the number of species of 33 functional groups with stages of forest succession. The number of species was predicted using a generalized linear mixed model with Poisson error and an observation-level random effect. Predictor variables were the forest successional stage as an unordered factor, elevation and soil parameters. For the predictions, elevation (800 m. a.s.l.) and soil parameters (mean value of the soil characteristics; PC1) were kept constant. Lines were generated by fitting a loess curve. Green lines indicate taxonomic groups whose number of species is significantly affected by the forest successional stage; orange lines indicate taxonomic groups whose number of species is not significantly affected by forest successional stage. Black bars indicate the standard error within each successional stage. Note that data were not available for some taxonomic groups in some successional stages. Abbreviations are explained in figure 2.2.1.

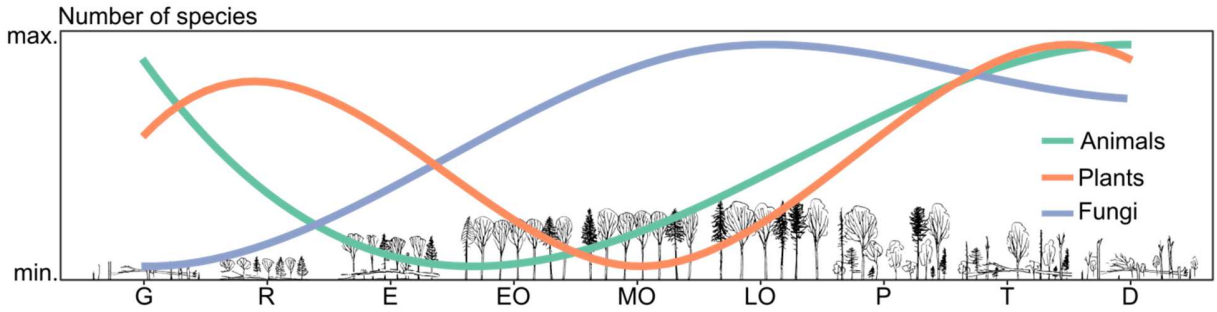

FIGURE 2.2.3. Normalized sum of predicted number of species along forest succession for the three kingdoms animals, plants and fungi. Lines were generated by fitting a loess curve. See figure 7.1.9 for absolute values. Note that this figure is based on all plots, while figure 7.1.9 is based on those plots that all taxa within the kingdom have in common. Abbreviations are explained in figure 2.2.1.

Results

Stages of forest succession

Plots were not equally distributed across successional stages (Fig. 7.1.3). The most prevalent stage (29% of 287 plots) was the mid-optimum stage, and the least prevalent stages (3%) were regeneration and plenter stages. Nevertheless, the distribution of plots across stages was representative for the Bavarian Forest National Park (Fig. 7.1.3; Spearman's $\varrho = 0.67$, $P < 0.05$). The successional stages differed in both elevation and soil characteristics (Figs. S7.1.4, 7.1.5; ANOVA: elevation $F_{8,278} = 19.8$, $P < 0.001$; soil $F_{8,278} = 5.06$, $P < 0.001$). Therefore, we used elevation and soil characteristics as control variables in the models of the number of species and abundance.

Abundance and number of species

The response of the abundance of several taxa of producers, first-order consumers, saprotrophs and saproxylic saprotrophs to forest succession yielded a U-shaped pattern. However, especially for taxa with low abundances or sample sizes, this response was not significant. We found no consistent response of higher-order consumers to forest succession (Table 7.1.2). Nevertheless, the effect of the quadratic term of stages of forest succession was predominantly positive, which indicated a U-shaped response of most taxa (27 of 33 functional groups).

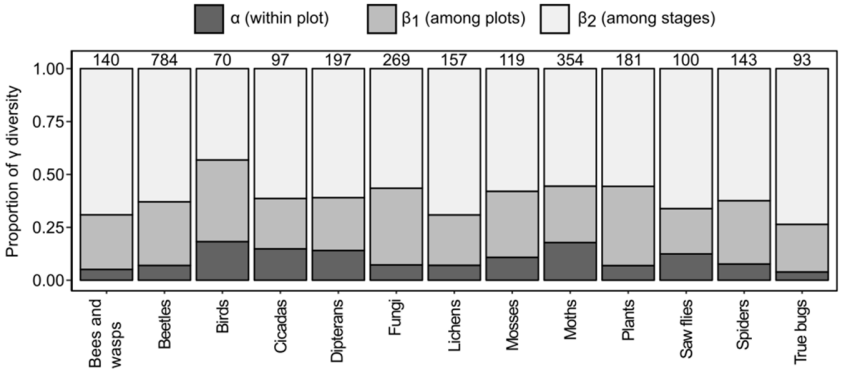

FIGURE 2.2.4. Proportion of γ-diversity due to α-diversity and β-diversity among plots and among stages of forest succession according to additive diversity partitioning. Results are based on presence–absence data for those taxonomic groups not separated into trophic levels with sufficiently high numbers of species (i.e. excluding taxonomic groups with ≤ 30 species). γ-Diversity for taxonomic groups is denoted above the respective bar.

We found a positive quadratic term for forest successional stage for the number of species of producers and the majority of consumer taxa, which indicated a U-shaped response to forest succession. However, the number of species of most of the saprotrophic taxa did not strongly change along forest succession. Furthermore, the response patterns of saproxylic beetles and fungi were equally strong but opposing, with a U-shaped response of beetles to forest succession and a hump-shaped response of fungi (Table 7.1.3, Fig. 2.2.2).

When we controlled for abundances of each group in the models of the number of species, we found that abundances were the strongest predictor for every taxon analyzed (Tables 7.1.3, 7.1.4). However, a few taxa showed significant responses to forest succession even after we controlled for effects of abundance. Here, forest succession had a positive linear effect on plants and saproxylic beetles, i.e. over the course of forest succession, the number of species increased. The positive quadratic term in the model indicated a U-shaped response of the number of species of phytophagous beetles, true bugs, cicadas, predatory spiders and dipterans to forest succession. By contrast, we found a negative quadratic relationship of the number of species of saprotrophic beetles and saproxylic fungi with forest succession, i.e. a hump-shaped response.

At the kingdom level, the number of plant species in the regeneration and establishment stages was particularly high, with a minimum in the optimum stages, and a secondary maximum in the terminal and decay stages of succession. Animals benefited from canopy openness, and the number of animal species in the gap stage was high, followed by a decrease in the number of species until the mid- to late-optimum stages and a subsequent increase towards the maximum number in the decay stage. The number of species of wood-inhabiting fungi and lichens steadily increased over the course of forest succession, saturating during the plenter stage (Fig. 2.2.3).

Species composition

Overall, we found high levels of species dissimilarity among plots for all taxa (Fig. 7.1.6). The Sørensen index of dissimilarity exceeded 90% as a result of high spatial turnover; nestedness never accounted for more than 6% of the overall dissimilarity (Fig. 7.1.6). Additive partitioning of the number of species showed that β-diversity among successional stages contributes most strongly to γ-diversity (Fig. 2.2.4). Multivariate analysis of variance on distance matrices of taxonomic groups showed significant differences in species composition between successional stages for all taxa (Table 2.2.1). When we visualized the change in species composition along the course of forest succession by using partial correspondence analysis, a "circular" pattern emerged, i.e. early and late stages of succession had similar species compositions (Fig. 2.2.5). Most unique species were found in the early and late stages of forest succession (Fig. 7.1.7).

Discussion

Following our initial hypothesis (H1), our results showed that abundances and number of species of most taxa largely follow a U-shaped pattern along forest succession (Fig. 2.2.2, Tables 2.2.1, 7.1.2). However, counter to our expectations, saprotrophic organisms did not show a hump-shaped response to forest succession, and saproxylic fungi showed a hump-shaped response and not a U-shaped response to forest succession, which indicates that this latter species group does not closely track the

accumulation of dead wood along forest succession. For most groups, the effect of forest succession was strongly affected by the abundances of the respective groups, which provides strong support for the more-individuals hypothesis (H2; Table 7.1.4). However, we found a response of several taxa to forest succession even after we controlled for the effect of abundance (Table 7.1.4). Overall, the diversity of plants, animals and fungi showed diverging patterns along forest succession, with peak diversity values in early and late stages (Fig. 2.2.3). We found the highest rates of species turnover among successional stages (Figs. 2.2.4, 7.1.7) and the most similar assemblages in early and late successional stages (open canopies) (H3; Fig. 2.2.5).

Stages of forest succession

Although the youngest and oldest successional stages of our study would appear to be different, they actually are almost the same because succession is cyclic. The generation of old trees decays contemporarily with the growth of a new generation. According to Fig. 7.1.2, the difference between the youngest and oldest stages in our study is in the 30% threshold of the canopy projection area. Nevertheless, the gap stage and the decay stage in our study differ markedly as the canopy projection area in the gap stage is considerably lower than in the decay stage (Fig. 7.1.11). Dead-wood volume is not included in our criteria for gaps and regeneration stages, although stands with low and high volumes of dead wood are dissimilar, especially for saproxylic species.

In our study, the forest successional stages establishment, late optimum and plenter were underrepresented due to forest history (Fig. 7.1.5). This highlights an important limitation of a space-for-time approach as applied here, which inter alia assumes that the analyzed stands have a consistent management and disturbance history (Dieler et al. 2017). Thus, particularly our results concerning these underrepresented stages should be interpreted with caution. Future analyses could supplement chronosequence data with simulation approaches to more explicitly study long-term trajectories of forest succession. In turn, the comprehensive dataset compiled here (Table 7.1.3) could be linked to simulation model output in future studies, quantifying how future forest development (influenced by changing climate and disturbance regime) impacts biodiversity (Thom et al. 2017). Our LiDAR approach revealed advantages but also limitations in the classification of successional stages, namely the ability to capture canopy closure across large spatial scales but the difficulty in characterizing the understory and downed dead wood. In this context, our results quantify the changes in biodiversity across forest succession and present a dynamic baseline for the monitoring of biodiversity change in temperate forests. Future changes (e.g. driven by changes in climate or land use), whether observed or projected, need to be considered in the light of the natural dynamics of forest succession, acknowledging that there are no static reference conditions for the diversity in temperate forests.

Ecology of taxa

Most taxa responded according to our predictions derived from the variation in critical resources across the stages of forest succession (cf. Figs. 2.2.1, 2.2.2). The high number of species of producers in both the early and late successional stages is most likely driven by shifts in primary production from trees to herbs, mosses and lichens, which depend on sunlight reaching the forest floor (Zehetgruber et al. 2017). This U-shaped response increases the

resource availability for phytophagous insects (Bouget & Duelli 2004). Previous analyses in our study region have shown that the number of species of several arthropod groups increases with forest development from closed forest to open canopies (Müller et al. 2008). For arthropods, this is partly an effect of increased activity of ectotherms under the higher temperatures associated with open habitats. However, our results indicate that for consumer groups, the effect of forest succession on the number of species is not only driven by more individuals, but also reflects an increase in habitat heterogeneity (Tables 7.1.2, 7.1.4). An increase in the abundance and number of species controlled for abundance of first-order consumers is frequently followed by an increase in the abundance of predators, such as spiders, beetles and birds, which results from bottom-up trophic interactions (Campbell & Donato 2014). However, we found that although the amount of dead wood was high on our study plots in early stages of forest succession (Fig. 7.1.11), this was not reflected in the number of species of wood-decaying (saproxylic) fungi.

TABLE 2.2.1. Effects of forest successional stages on species composition. Results from a multivariate analyses of variance using distance matrices (Adonis) based on presence–absence data. Significance was tested using 999 permutations. Those taxonomic groups not separated into trophic levels and with sufficiently high numbers of species (i.e. excluding taxonomic groups with ≤ 30 species) were analyzed. R^2, coefficient of determination; soil, soil parameters of the plots. Significant effects are indicated by bold typesetting.

				P-value		
Taxon	**Plots (n)**	**Species (n)**	***R²***	**Forest successional stage**	**Elevation**	**Soil**
Lichen	109	157	0.25	**<0.001**	**0.004**	0.755
Mosses	109	119	0.20	**<0.001**	**<0.001**	**<0.001**
Plants	282	181	0.24	**<0.001**	**<0.001**	**<0.001**
Cicadas	36	95	0.36	**0.009**	**0.003**	0.120
Beetles	178	783	0.21	**<0.001**	**<0.001**	0.066
Birds	283	72	0.19	**<0.001**	**<0.001**	**0.003**
Moths	35	354	0.33	**0.009**	**<0.001**	0.524
Sawflies	35	100	0.33	**0.003**	0.066	0.084
Spiders	173	143	0.29	**<0.001**	**<0.001**	**0.016**
True bugs	150	93	0.14	**<0.001**	**0.002**	0.142
Dipterans	36	197	0.33	**<0.001**	**0.005**	0.059
Bees and wasps	142	140	0.14	**<0.001**	**<0.001**	0.638
Fungi	286	269	0.20	**<0.001**	**<0.001**	**0.015**

This is consistent with the more detailed analyses of Krah et al. (2018), which show that the mere amount of dead wood is a relatively poor predictor of the number of these fungal species. The number of fungal species might be driven more strongly by the host tree species, host size, dieback history and canopy openness than by the amount and heterogeneity of dead wood (Abrego and Salcedo 2013, Heilmann-Clausen et al. 2015, Krah et al. 2018).

Ecological mechanism: more-individual hypothesis and habitat heterogeneity hypothesis

With regard to the mechanisms driving biodiversity in temperate forests, our results suggest

that the increase in the number of species is largely based on higher abundances, as predicted by the more-individuals hypothesis. However, after controlling for abundances, the number of species of species-rich groups, such as beetles, true bugs, cicadas, spiders and fungi, were still affected by the forest successional stages, which indicates variation in habitat heterogeneity in the form of host plants, microstructures or microclimates by facilitating coexistence, increasing niche space, and reducing local extinction risks (Stein and Kreft 2015). Increased canopy openness in early and late successional stages (Fig. 7.1.11) results in an increase in the number of species of vascular plants and mosses (Fig. 2.2.3) owing to the occurrence of pioneer species with low shade tolerance. However, when we controlled for the effect of abundances, vascular plants showed a linear response to forest succession, which indicated that in early stages, the increase in the number of species is mainly driven by denser understory vegetation and thus more individuals, rather than by habitat heterogeneity. The positive effect of forest succession on the abundance of vascular plants (Table 7.1.3) subsequently increases the diversity of herbivorous insects following the resource availability hypotheses. This increase in prey species might also support more predatory species. This interpretation is supported by the observed increase in the number of species of higher-order consumers after we controlled for abundances. High turnover rates between stands, as in our study (Fig. 7.1.6), can be driven by sampling effort, with higher turnover rates with lower sampling effort locally, but also can occur because of ecological differences between stands. Our present study showed that species turnover along successional stages contributed most strongly to the overall γ-diversity (Fig. 2.2.4). This indicates that for the promotion of forest diversity at the landscape scale, heterogeneity in forest successional stages is more important than within-stand heterogeneity, which is in accordance with the results of another recent multi-taxon analysis of forest diversity in Europe's temperate forests (Schall et al. 2017).

Implications for forest management

Based on our finding that both α-diversity and the number of unique species is highest in early and late stages of forest succession (Figs. 2.2.2, 2.2.3, 7.1.7, 7.1.10), we recommend that conservation efforts focus on these particular stages, which are currently underrepresented in Europe (Fig. 7.1.8). Late successional stages cannot be produced artificially but have to develop naturally over long time periods (but see Speight 1989 and Sebek et al. 2013 for techniques inducing premature senescence). α-diversity can be promoted in the short term by creating and maintaining early stages of succession, and this is an important option for ecosystem management (for experimental evidence, see Sebek et al. 2015). Canopy openings are a frequent result of logging activities, but these openings often lack the dead-wood resources required by many saproxylic taxa (Heikkala et al. 2016).

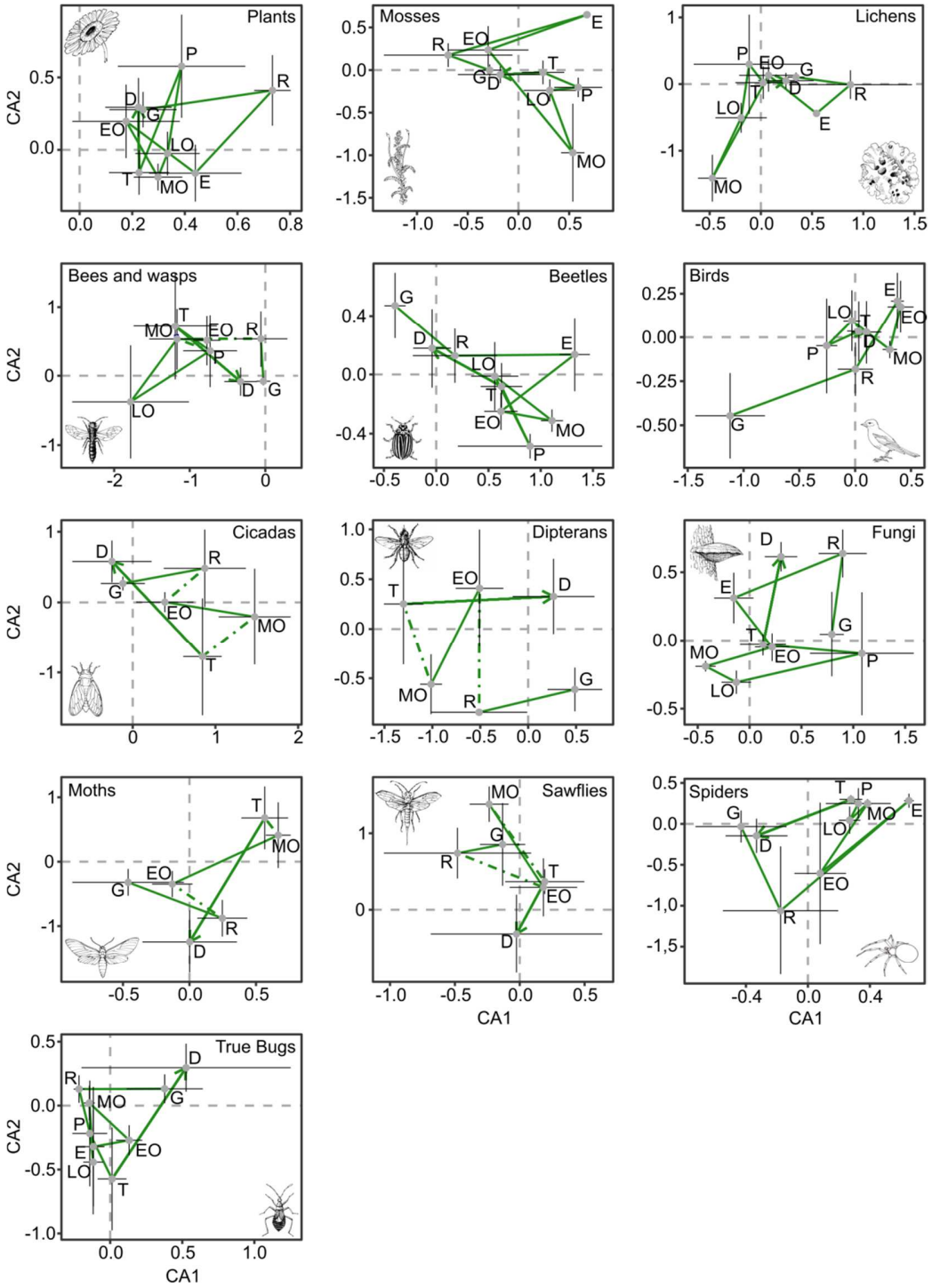

Figure 2.2.5. Partial correspondence analyses visualizing the response of species composition to forest succession. Results are based on presence–absence data for those taxonomic groups not separated into trophic levels with sufficiently high numbers of species (i.e. excluding taxonomic groups with ≤ 30 species). Multivariate analysis of variance on distance matrices for the taxonomic groups showed significant differences in species composition between forest successional stages for all taxa (Table 2.2.1). Arrows indicate pathways along successional stages, black bars indicate the standard error within each stage and green lines represent a significant influence of forest successional stage on species assemblages. Missing or underrepresented stages are marked with a green dashed line. CA1, first axis of correspondence analysis; CA2, second axis of correspondence analysis. Abbreviations explained in figure 2.2.1.

Based on our findings, we recommend that in silviculture, the canopy should be opened by, e.g. creating gaps, to increase the photosynthetically active radiation at the forest floor, and some dead wood should be retained on site.

Because intermediate successional stages also support a wide variety of taxa and communities, especially plants, fungi and lichen, a comprehensive conservation strategy has to maintain all successional stages on the landscape. However, for the conservation of regional biodiversity in multifunctional forests in Europe, this would mean that the proportion of stands in early and late successional stages should be increased.

All our implications only apply to the system we investigated, namely mixed mountain forests. However, more than half of Central Europe consists of mountain areas and most of the existing forests are concentrated there (CIPRA 2007). Moreover, other studies have shown similar results on the uniqueness of, e.g. the early successional stages (e.g. Jacobs et al. 2007, Tikkanen et al. 2007, Swanson et al. 2011), which suggests a further transferability of our results to other forests systems across Europe or temperate mountain forests of other continents.

Acknowledgments

TH and NF received scholarships from the Rudolf and Helene Glaser Foundation organized in the "Stifterverband für die deutsche Wissenschaft". RS acknowledges support from the Austrian Science Fund FWF through START grant Y 895-B25.

Chapter 2.3

Arthropod communities in fungal fruitbodies are weakly structured by climate and biogeography across European beech forests

with

Jörg Müller | Pablo Aramendi | Claus Bässler | Martin Brändle | Christophe Bouget | Antoine Brin | Heinz Bussler | Kostadin B. Georgiev | Radosław Gil | Martin M. Gossner | Jacob Heilmann-Clausen | Gunnar Isacsson | Anton Krištín | Thibault Lachat | Laurent Larrieu | Elodie Magnanou | Alexander Maringer | Ulrich Mergner | Martin Mikoláš | Lars Opgenoorth | Jürgen Schmidl | Miroslav Svoboda | Simon Thorn | Kris Vandekerkhove | Al Vrezec | Thomas Wagner | Maria-Barbara Winter | Livia Zapponi | Roland Brandl | Sebastian Seibold |

published in Diversity and Distributions, 25(5), 2019, p. 783-796

This paper is the follow-up to a pilot study I did during my M.Sc. studies. In the follow-up study, the conceptual framework was strongly developed, new data were collected, the analysis methodology completely revised and a new manuscript was written. Accordingly, this paper is a new scientific contribution to which I myself contributed the main part as lead author. For this chapter, there is a digital supplement with additional data on the enclosed compact disk.

Summary

The tinder fungus *Fomes fomentarius* is a pivotal wood decomposer in European beech *Fagus sylvatica* forests. The fungus, however, has regionally declined due to centuries of logging. To unravel biogeographical drivers of arthropod communities associated with this fungus, we investigated how space, climate and habitat amount structure alpha- and beta-diversity of arthropod communities in fruitbodies of *F. fomentarius*. We reared arthropods from fruitbodies sampled from 61 sites throughout the range of European beech and identified 13 orders taxonomically or by metabarcoding. We estimated the total number of species occurring in fruitbodies of *F. fomentarius* in European beech forests using the Chao2 estimator and determined the relative importance of space, climate and habitat amount by hierarchical partitioning for alpha-diversity and generalized dissimilarity models for beta-diversity. A subset of fungi samples was sequenced for identification of the fungus' genetic structure. The total number of arthropod species occurring in fruitbodies of *F. fomentarius* across European beech forests was estimated to be 600. Alpha-diversity increased with increasing fruitbody biomass; it decreased with increasing longitude, temperature and latitude. Beta-diversity was mainly composed by turnover. Patterns of beta-diversity were only weakly linked to space and the overall explanatory power was low. We could distinguish two genotypes of *F. fomentarius*, which showed no spatial structuring. *F. fomentarius* hosts a large number of arthropods in European beech forests. The low biogeographical and climatic structure of the communities suggests that fruitbodies represent a habitat that offers similar conditions across large gradients of climate and space, but are characterized by high local variability in community composition and colonized by species with high dispersal ability. For European beech forests retention of trees with *F. fomentarius* and promoting its recolonization where it had declined seems a promising conservation strategy.

Introduction

Most parts of the temperate zone of Europe - from the Iberian Peninsula to the Black Sea and from southern Italy to southern Sweden - are naturally covered by forests dominated by European beech *Fagus sylvatica* (Fig. 2.3.1). These forests, however, have declined over recent centuries due to deforestation until around 1800, and since then due to conversion to conifer-dominated (*Pinus sylvestris*, *Picea abies*) plantations (Dirkx 1998, Schelhaas et al. 2003). Historic deforestation and degradation have recently been reinforced by large-scale clear-cutting of old-growth beech forests in regions that, until recently, were rather unaffected (e.g. in the Carpathians; Vanonckelen and Rompaey 2015, Mikoláš et al. 2017). Since the distribution of European beech is restricted to the temperate zone of Europe, the EU has acknowledged its global responsibility by listing several types of beech forest as Natura 2000 habitats (Council of the European Union 1992). Furthermore, some of the last natural or almost natural European beech forests are part of the UNESCO World Heritage "Ancient and Primeval Beech Forests of the Carpathians and Other Regions of Europe" (http://whc.unesco.org/en/list/1133). Despite these commitments to conserving biodiversity in European beech forests, our understanding of large-scale drivers of biodiversity in beech forests remains limited, hampering systematic conservation planning, given prevalent area-conflicts (Margules and Pressey 2000, Kouki et al. 2012, Ammer et al. 2018).

The species pool of organisms associated with European beech forests can be expected to be structured across large spatial scales reflecting different underlying mechanisms. European beech was one of the last tree species to recolonize Central and Northern Europe from its major refugia in Southern Europe after the last glaciation and is still expanding its range towards the north and east (Magri 2008). Understory plant diversity in European beech forests reflects this history, and is determined by distance to the nearest known major refuge (Willner et al. 2009, Jiménez-Alfaro et al. 2018). In addition, populations of European beech may also have persisted in microrefugia in Central Europe (Robin et al. 2016). Due to its high competitiveness and climate tolerance, European beech covers a wide range of climatic conditions (Fig. 2.3.1; Brunet et al. 2010), which might structure communities (Heilmann-Clausen et al. 2014). Towards its ecological range limits, increasing presence of other tree species and arthropods associated to these trees (Brändle and Brandl 2001a) may further influence the regional species pool.

These natural drivers of community structure in beech forests interact with anthropogenic factors. Forest clearing and forest management have been more intense in Western than in Eastern Europe resulting in a gradient of habitat loss of natural beech forest and consequently fragmentation of these forests from east to west (Larsson 2001, Kaplan et al. 2009, Abrego et al. 2015).

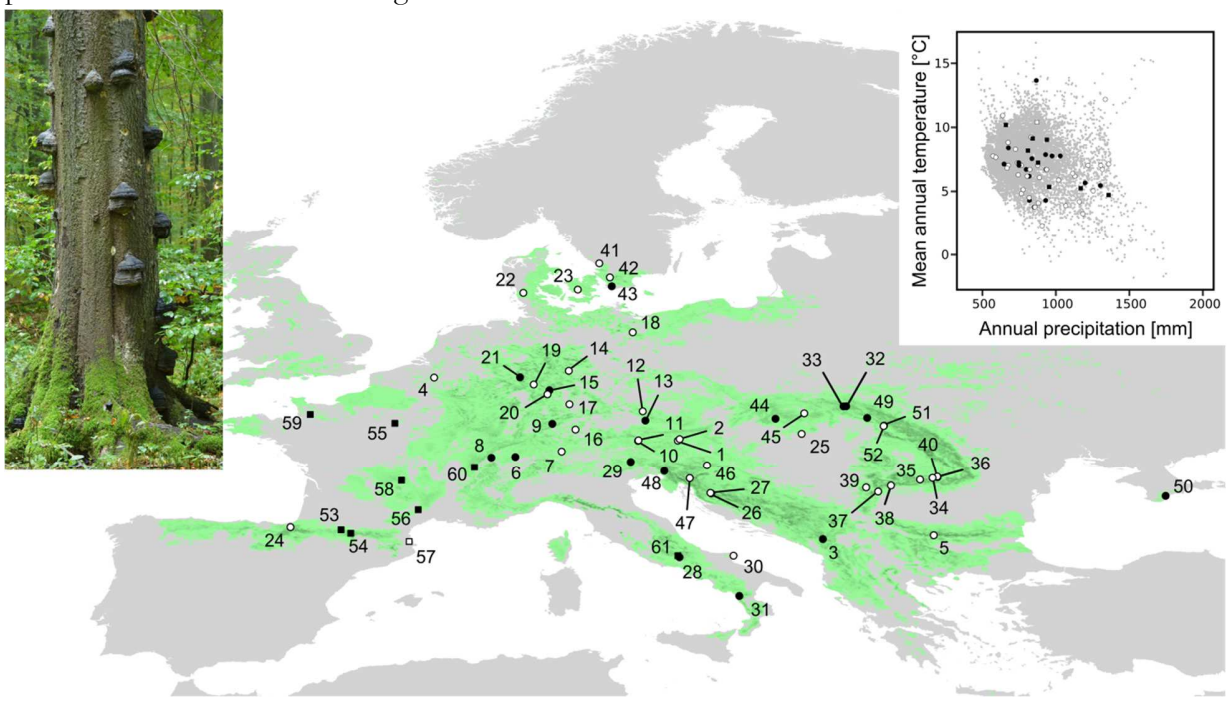

FIGURE 2.3.1. Map of the 61 sampling sites of this study. The green area depicts the predicted current distribution of European beech *Fagus sylvatic*a (Brus et al. 2011). The numbers in the map correspond to the study site ID in Tables 7.2.1, 7.2.2 and 7.2.3. Circles indicate the 52 study sites for which data on all arthropods were available; squares indicate the 9 sites for which only beetle data was available and which are part of the analyses in chapter 7.2. Black filling indicates sites with active forest management and white filling indicates unmanaged sites. Left inset: A typical example of a European beech tree with fruitbodies of *Fomes fomentarius*. Photograph by Thomas Stephan. Right inset: Mean annual temperature and annual precipitation of all study sites (filled circles and squares see above) and 10,000 randomly sampled points in the distribution of *F. sylvatica* representing the climate space where beech-dominated forests are occurring.

Many specialist species for old-growth beech forests have thus become rarer or locally extinct in Western Europe and can today only be found in Eastern Europe (Speight 1989, Eckelt et al. 2018).

On smaller spatial scales, species communities can be affected by the regional climate acting as environmental filter as shown for wood-inhabiting beetles and fungi in beech forests (Bässler et al. 2010a, Müller et al. 2013) and minute tree-fungus beetles in fruitbodies (Reibnitz 1999). Moreover, not only large-scale gradients of anthropogenic pressure can influence communities in beech forests but also the amount of available habitat at local and landscape scales (Bässler et al. 2010a, Müller et al. 2013) and the connectivity of habitat patches (Rukke 2000, Abrego et al. 2015, Nordén et al. 2018).

Fungi are the main biotic agents of wood decomposition and their mycelia and fruitbodies are an important food for many arthropods as they contain higher concentrations of nutrients stored in a more accessible form than in undecayed wood (Merrill and Cowling 1966, Stokland et al. 2012, Filipiak et al. 2016). In particular, fungal fruitbodies, especially polypores, serve as habitat for many fungicolous arthropod species (Schigel 2012). Studies of the diversity and composition of fungicolous arthropod communities have so far been restricted to local and regional scales, and generally indicate that many arthropod species are host-specific (Komonen 2001, Jonsell and Nordlander 2004). Occurrence and abundance of fungicolous arthropod species on single trees and forest stands depend on habitat availability (Rukke 2000). At the regional scale, turnover in species composition has been found to be high among fungal host species, but low among sites across host species (Komonen 2001). So far, no study has investigated diversity patterns of fungicolous arthropods at continental scales (Schigel 2012).

The tinder fungus *Fomes fomentarius* is one of the main decomposers of wood in many beech forests in Europe. However, *F. fomentarius* has a much larger range than European beech covering the temperate and boreal zones of Europe, Asia and North America. Outside beech forests, it occurs especially in riparian and boreal forests on Betula, Populus, Alnus or other hardwood trees (Matthewman and Pielou 1971, Reibnitz 1999, Rukke 2000). As a white-rot fungus, it can efficiently break down ligno-cellulose and contributes to the death of weakened living trees, thus promoting natural forest dynamics (Butin 1989). Its fruitbodies and the created dead wood are habitat for many arthropod species (Schigel 2012). Their community composition is largely affected by the physical conditions of the fruitbodies which change with ongoing decomposition (Matthewman and Pielou 1971, Reibnitz 1999, Rukke 2000). Thus, in order to capture the whole local community occurring in *F. fomentarius*, different stages of decomposition have to be taken into account (Graves 1960).

Trees colonized by the fungus have been suggested as a focal habitat for biodiversity conservation in beech forests (Müller 2005, Larrieu et al. 2018). However, due to centuries of logging and direct persecution for phytosanitary reasons, populations of this fungus have declined or became locally extinct in many areas (Vandekerkhove et al. 2012, Zytynska et al. 2018). To guide conservation planning and strategies in European beech forests, such as the selection of areas to be set aside for conservation (Bouget et al. 2014) or for active restoration by dead-wood enrichment (Dörfler et al. 2017), it is necessary to understand how arthropod communities – which represent the largest fraction

of animal biodiversity in forests – are biogeographically structured.

In this study, we reared arthropods from fruitbody samples of *F. fomentarius* across the whole distributional range of European beech. Our aims were to estimate alpha- and beta-diversity of arthropods in fruitbodies of *F. fomentarius* and to disentangle the effects of postglacial recolonization of its host tree, macro-climate, anthropogenic pressure and habitat amount on diversity patterns. Specifically, we expected (i) decreasing alpha-diversity and increasing nestedness with latitude due to the recolonization history of beech, (ii) decreasing alpha-diversity and increasing nestedness from east to west due to the anthropogenic land-use history, (iii) increasing turnover with increasing differences in macro-climatic conditions across both latitudinal and longitudinal space, and (iv) increasing alpha-diversity with increasing habitat amount at local and landscape scales.

Methods

Collection of Fomes fomentarius fruitbodies

We collected fruitbodies from 61 beech-dominated forest sites across the distributional range of *F. sylvatica* (Fig. 2.3.1) between June and August 2013. These sites were chosen to cover the natural distribution of *F. sylvatica*, as well as the full range of climatic conditions within this area (Fig. 2.3.1). We were not able to include sites from some parts of the distribution range, e.g. Southern England, where *F. fomentarius* is almost absent for historical reasons (Abrego et al. 2017). Sites were located in unmanaged (36) and managed forests (25); both management categories were evenly distributed across Europe (Fig. 2.3.1).

For arthropod rearing, we collected 10 fruitbodies of *F. fomentarius* per site following a standardized protocol. Assemblages inhabiting fruitbodies of bracket fungi change with ongoing fruitbody decomposition. Therefore, we sampled fruitbodies at different successional stages of decay. At each site, sampling included fruitbodies attached to wood that had just recently died and were still moist (3 to 4 fruitbodies) and fruitbodies that had been dead for a longer time (6 to 7 fruitbodies). The latter were either dry when still attached to wood (3 to 4 fruitbodies) or wet when lying on the ground (3 to 4 fruitbodies). This sampling protocol aimed at covering most of the available habitat heterogeneity represented by the fruitbodies. The total volume sampled per site ranged between 0.2 and 21.7 kg (mean: 2.7 kg) and did not represent the local availability of fruitbodies as transportation and rearing logistics restricted the sampled volume.

In addition, we collected samples of living fruitbodies to analyze the genetic structure within the population of *F. fomentarius* in Europe. From these samples, we applied a microwave-based method to extract DNA (Dörnte & Kües 2013) and amplified sequences for the internal transcribed spacer (ITS) region and the elongation factor α (efa) gene by touchdown PCR (for details, see chapter 7.2).

Arthropod rearing

To rear arthropods, all fruitbodies of the same site (from now on called 'sample') were put into a cardboard box (25 cm x 25 cm x 50 cm) in an unheated well-ventilated storage room with a seasonal temperature regime. A transparent collecting jar was attached to each box and filled with 90% ethanol to collect arthropods attracted to light. Collecting jars were emptied every two months and arthropods inside the boxes were collected by hand. Rearing was carried out for 12 months for each sample.

Arthropod identification and classification

Reared arthropod specimens were stored in ethanol and beetles were determined to species level by taxonomists. The remaining fauna was identified by metabarcoding using next generation sequencing carried out by Advanced Identification Methods GmbH (Munich, Germany; for details, see chapter 7.2). Arthropod sequences were matched against the publicly available DNA barcode library within the Barcode of Life (BOLD – v4.boldsystems.org; Ratnasingham and Hebert 2007). Lab problems impeded the use of next-generation sequencing for samples from nine sites (Fig. 2.3.1).

We considered all species that were reared from fruitbody samples, including species that use hollow fruitbodies as shelter or develop at the interface between fruitbodies and white-rotten wood. However, since this includes species that do not interact directly with the fruitbody, we additionally analyzed the data excluding these species. Based on literature, we classified species or genera that are known to feed directly on the fungal tissue or exclusively prey upon mycetophagous species as 'fungi specialists' (see chapter 7.2); and we classified all species according to their trophic level as consumers (i.e. species that feed on non-animal tissue), predators (i.e. species that feed on animal tissue) or parasitoids (i.e. species that develop on or within single host organisms and ultimately kill their host).

Environmental predictor variables

Coordinates of each site were recorded in the field using handheld GPS devices (Table 7.2.3). We extracted data on all 19 bioclimatic variables for each site from the WorldClim database (Hijmans et al. 2005). Since bioclimatic variables are often correlated, we performed a principal component analysis on the correlation matrix for temperature and precipitation variables separately (i.e. temperature: BIO 1 – 11; precipitation: BIO 12 – 19). The first two principal components explained most of the variation in both datasets (temperature: 75%; precipitation: 91%; Table 7.2.4) and were subsequently used as a proxy for bioclimatic conditions at the sites. The first principal components represented a gradient in mean temperature or precipitation with high values indicating sites with overall high temperature or sums of precipitation, respectively. The second principal components represented a gradient in seasonality with high values for sites displaying high temperature or precipitation seasonality, respectively.

To obtain a proxy for landscape-scale habitat amount and anthropogenic pressure, we calculated the proportion of forest cover surrounding the sites for radii from 100 to 5000 m (100 m steps). Forest cover within a radius of 700 m around sites had the highest independent effect on alpha-diversity and thus this radius was chosen for further analyses (Fig. 7.2.2). We used data based on Landsat satellite images from the database on Global Forest Change (Hansen et al. 2013), which is available with a spatial resolution of approximately 25 meters per pixel, with values ranging from 0 to 100 per pixel encoding the proportion of canopy closure for all vegetation taller than 5 m in height. To evaluate the role of sample size (as a proxy for local habitat amount) for alpha- and beta-diversity, we recorded the total dry weight of fruitbodies per sample after 12 months of rearing. Proportions of forest cover were logit-transformed and sample size was $\log_e$-transformed.

Statistical analyses

All statistical analyses were carried out using R version 3.4.3 (R Core Team 2017). The main analyses included beetles identified taxonomically and all other arthropods identified by metabarcoding and were thus restricted to the 52 sites for which metabarcoding data were available. Additional analyses were conducted for beetle data from all 61 sites with beetle abundances (see chapter 7.2).

To estimate the overall species pool, we calculated the Chao2 estimator, as implemented in the vegan package version 2.4-3 (Oksanen et al. 2018). The Chao2 estimate is a function of species occurring once or twice in the dataset and offers robust lower bound estimation for species richness based on incidences under the assumption that rare species have similar detection probabilities (Chao 1987). Calculations were based on data for all species and separately for fungi specialists and each trophic guild (i.e. consumer, predator and parasitoid) on the 52 sites. In addition, we used the rarefaction-extrapolation framework based on species incidences across all sites (Chao et al. 2014). We used Hill number of the orders 0 (species richness), 1 (the exponential of Shannon's entropy), and 2 (the inverse of Simpson's concentration) to analyze the diversity of rare and common species within one framework. We used 999 replicated bootstraps to calculate confidence intervals around the species-accumulation curves using the iNEXT package (Hsieh et al. 2016).

Alpha-diversity was calculated as the number of species per site. To estimate the relative importance of the predictor variables, we performed hierarchical partitioning – as implemented in the hier.part package version 1.0-4 (Walsh & Mac Nally 2013) – based on generalized linear models. For the generalized linear models, we chose a quasipoisson error distribution and a log-link function in order to account for frequently observed overdispersion in models of count data. Please note, that alternatively choosing models including an observation-level random effect or models with a negative-binomial error distribution did not alter the main results. The models included alpha-diversity as the dependent variable and space (latitude, longitude), climate (mean temperature, temperature seasonality, mean precipitation, precipitation seasonality) and habitat amount (forest cover, sample size) as predictor variable sets. All calculations were performed separately for all species, fungi specialists and each trophic guild on the 52 sites.

Beta-diversity was calculated as the Sørensen dissimilarity among all 52 sites using presence-absence information. The community composition of all species and fungi specialists was visualized using non-metric multidimensional scaling (NMDS). Subsequently, we fitted the environmental vectors of space, climate and habitat amount to the resulting ordination as implemented in the envfit function using the vegan package. In addition, we performed an analysis of similarity in order to test for group differences in community composition among managed and unmanaged sites, as well as among biogeographic regions again using vegan (see chapter 7.2 for further details). Furthermore, we decomposed beta-diversity in its turnover and nestedness components based on the Sørensen index family as implemented in betapart (Baselga et al. 2017). The turnover component represents beta-diversity introduced by the replacement of species between sites, while the nestedness component represents the beta-diversity introduced by the removal/gain of species between sites. To estimate the relative importance of the predictor variables (latitude, longitude, mean

temperature, temperature seasonality, mean precipitation, precipitation seasonality, forest cover and sample size) for beta-diversity, we calculated generalized dissimilarity models (GDM) as implemented in the gdm package (Manion et al. 2017) for total beta-diversity, and turnover and nestedness components separately. GDMs allow the analysis of spatial patterns of community composition across large regions under consideration of non-linear relationships between dissimilarity in community composition along environmental gradients (Ferrier et al. 2007). All GDMs were calculated using the default of three I-splines. The calculated coefficient for each of the three I-splines represents the rate of change along a third of the gradient of the environmental predictor when keeping all other predictors constant (i.e. high values of the first I-spline indicate a high rate of change along the first third of the gradient). We estimated the relative contribution of each predictor set as the difference in explained deviation between a model containing all predictor sets and a model from which this predictor set was removed (Legendre and Legendre 2012, Maestri et al. 2017). All calculations were again performed separately for all species, fungi specialists and each trophic guild on the 52 sites.

Data for beetles including abundances were available for all 61 sites; we thus conducted similar analyses for this group as for all arthropods (see chapter 7.2). These analyses considered the influence of increasing numbers of individuals on alpha-diversity and the effect of space, climate and habitat amount on abundance-based dissimilarities of the beetle communities. Here, we used Bray-Curtis-dissimilarities and decomposed it into the two components based on balanced variation in abundance (i.e. individuals of some species at a site are substituted by equal numbers of individuals at another site) and dissimilarity introduced by abundance gradients (i.e. individuals are lost without substitution from one site to the other; Baselga 2013).

Results

In total, we identified 216 arthropod species emerging from fruitbodies of *F. fomentarius* from 52 sites. Species belonged to 13 orders, with highest species richness found in Diptera (n = 72) and Coleoptera (n = 71; Fig. 2.3.2; see Digital Supplementary). The majority of taxa (n = 179) could be assigned to species by the taxonomist or by alignment of operational taxonomic units (OTUs; see chapter 7.2) with existing databases. The remaining 37 OTUs not assigned to a species were mostly members of the Cecidomyiidae (Diptera), for which barcodes were not available in the databases. We identified 74 species as fungi specialists. Concerning trophic guilds, we classified 131 species as consumers, 68 species as predators and 17 species as parasitoids.

Genetic analysis of *F. fomentarius* samples revealed two genotypes that were previously identified as possible sympatric cryptic species (termed genotype "A" and "B"; Judova et al. 2012). However, intraspecific genetic variation among sites was very low and genotype B occurred only at five of our sites widely spread over the sampling area (see chapter 7.2.).

Chao2 estimators indicated an overall species pool of 587 (SE = 103) for all species, 249 (SE = 181) for fungi specialists, 402 (SE = 104) for consumers, 163 (SE = 43) for predators and 42 (SE = 24) for parasitoids associated with *F. fomentarius* in European beech forests. The observed effective number of typical species (q = 1) was 87, while the observed effective number

of dominant species (q = 2) was 44 (Fig. 7.2.4). Many of the dominant species were consumers, such as beetles of the family Ciidae, the Tenebrionidae *Bolitophagus reticulatus*, the micro-moth *Scardia boletella* and Cecidomyiidae sp.3 (Fig. 2.3.3). The most frequent parasitoids were the hymenopterans *Astichus* spp. and a scuttle fly (Phoridae). Beetles included four species considered to be "primeval forest relicts" (Eckelt et al. 2018), namely *Bolitophagus interruptu*s, *Bolitochara lucida*, *Teredus cylindricus* and *Phillothermus evanescens*, which were each found at one site (Slovenia, France, southern Italy and Sweden, respectively).

Considering all arthropods, the mean species number per site was 16 (SE = 6) with the lowest number (6 species) found in the German Wetterau and the highest number (36 species) located in Abruzzo, Italy. In the Quasipoisson-models, our predictor variables explained 20% of the deviance in alpha-diversity for all species and 26% for the fungi specialists (Fig. 2.3.4). The explained deviance decreased from consumers (22%) to predators (16%) and parasitoids (6%) correlated to the number of species of the trophic guilds (Table 2.3.1). According to hierarchical partitioning, habitat amount, i.e. forest cover and sample size, explained most of the deviance in our models (Fig. 2.3.4). Alpha-diversity of all species, fungi specialists, consumers and predators increased with increasing sample size (Table 2.3.1, Fig. 2.3.5A) and that of consumers also increased with increasing forest cover. Moreover, alpha-diversity of all species, fungi specialists and consumers decreased with increasing longitude and that of fungi specialists also decreased with latitude. Alpha-diversity of fungi specialists and consumers additionally decreased with increasing mean temperature and precipitation (Table 2.3.1). Most effects, however, were only marginally significant (Table 2.3.1).

Ordination of the community composition of all species as well as fungi specialists revealed large differences in community composition across our study sites (Fig. 7.2.3). Except for a significant effect of sample size on the community composition of all species ($r^2 = 0.13$, $p < 0.05$), environmental variables were not significantly correlated with the axes of the NMDS (Fig. 7.2.3 A & D). In addition, we found no differences in community composition among managed and unmanaged sites, as well as among biogeographic regions (Fig. 7.2.3). The largest proportion of dissimilarity was due to turnover, rather than nestedness for all species (98%), fungi specialists (96%) and all trophic guilds (consumer: 97%; predator: 99%; parasitoids: 97%).

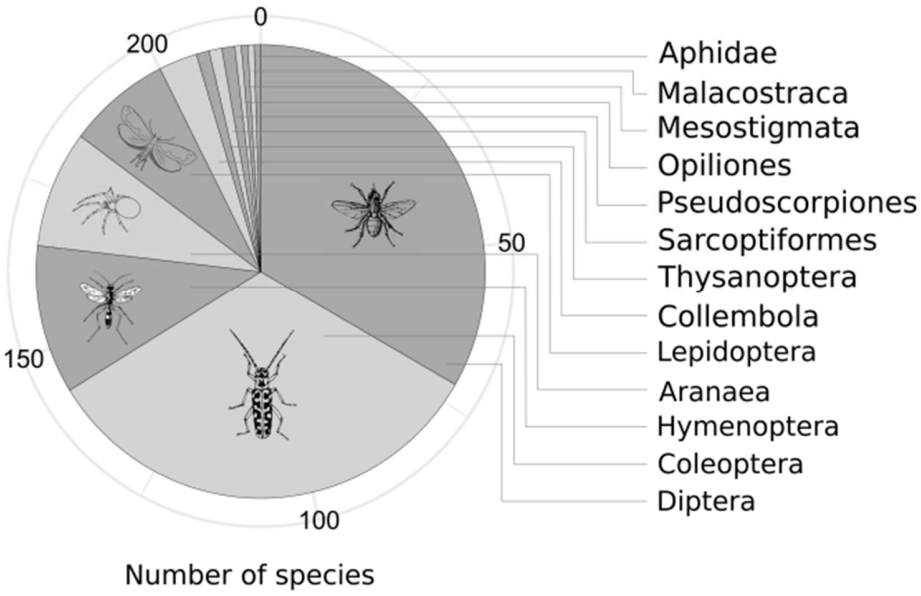

FIGURE 2.3.2. Pie chart of the proportion of species from different arthropod orders reared from fruitbodies of *Fomes fomentarius* from 52 beech-dominated forest sites across Europe. The overall number of determined species was 216.

The proportion of deviance explained by GDMs was below 15% for overall beta-diversity, nestedness and turnover in all groups (Fig. 2.3.4). For all species, we found a marginally significant increase of dissimilarity introduced by nestedness with increasing longitudinal distance between sites (Table 2.3.2). No single predictor had a significant effect on beta-diversity of fungi specialists and consumer species (Table 7.2.5 & Table 7.2.6). Dissimilarity in latitudinal distance had a significant positive effect on the overall beta-diversity as well as on the turnover component for predators and parasitoids (Table 7.2.7 and Table 7.2.8). Additionally, we found a significant increase in overall beta-diversity as well as in dissimilarity due to turnover with increasing dissimilarity of sample size for predators.

Our analyses for beetles from all 61 sites included abundance data for 123 species (Digital Supplementary). Here, alpha-diversity was strongly affected by sample size (Fig. 2.3.5; Table 7.2.12). The number of beetle species increased with fungal sample size as the range in sample size was considerably higher across all 61 sites (Fig. 2.3.5B) than across the subset of 52 sites (Fig. 2.3.5A). Beetle community composition was affected by dissimilarity in sample size and longitude. Here, beetle communities showed increased rates of turnover and balanced changes of abundances with longitude and increased rates of nestedness and abundance-gradients with sample size.

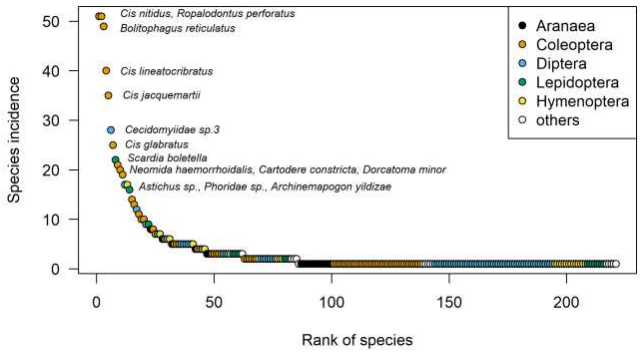

FIGURE 2.3.3. Rank-incidence plot of all 216 arthropod species reared from fruitbodies of *Fomes fomentarius* from 52 beech-dominated forest sites across Europe.

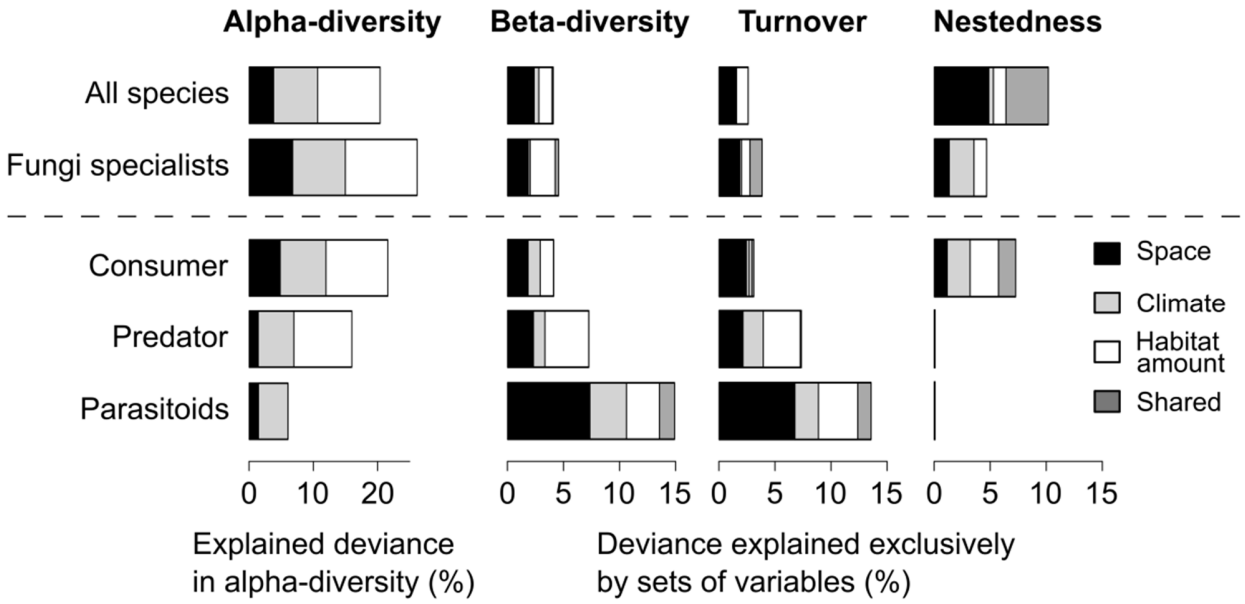

FIGURE 2.3.4. Relative contribution of predictor sets in explained deviance of alpha- and beta-diversity and its components turnover and nestedness. Alpha-diversity was modeled using generalized linear models and the relative contribution is based on hierarchical partitioning. Beta-diversity is based on presence-absence data and its components were modelled using generalized dissimilarity models and the relative contribution was calculated as the 'pure' effect of the predictor set on the overall explained deviance of the model. All analyses were conducted for all species and fungi specialists separately and for the trophic levels consumer, predator and parasitoids. Bar colors represent the predictor sets with space in black, climate in light grey, habitat amount in white and the deviance shared by the predictors in dark grey.

TABLE 2.3.1. *Z*-values and explained deviance of generalized linear models (quasipoisson-family) with the number of species of all species or within guilds as response variables. Significant effects are indicated by bold typesetting. PC1 and PC2 refer to the first two axes of the respective principal component analyses of temperature or precipitation variables (see *Methods*).

Predictor set	Predictor	All species	Fungi specialists	Consumer	Predator	Parasitoids
Space	Latitude	-1.36	**-1.98 .**	**-1.70 .**	-0.08	-0.93
	Longitude	**-1.77 .**	**-2.12 ***	**-1.82 .**	-1.08	-0.34
Climate	Temperature (PC1)	**-1.72 .**	**-1.90 .**	**-1.92 .**	-0.48	-1.00
	Temperature (PC2)	-0.82	-0.79	-0.43	-1.24	0.31
	Precipitation (PC1)	-1.41	-1.30	-1.57	-0.68	-0.01
	Precipitation (PC2)	-0.31	0.13	-0.45	0.74	-1.49
Habitat amount	Forest cover	1.26	0.94	1.45	0.13	-0.13
	Sample size	**1.75 .**	**2.20 ***	1.55	**2.20 ***	0.17
Explained deviance		0.20	0.26	0.22	0.16	0.06

Notes. Significance levels: * $P < 0.05$, . $P < 0.1$

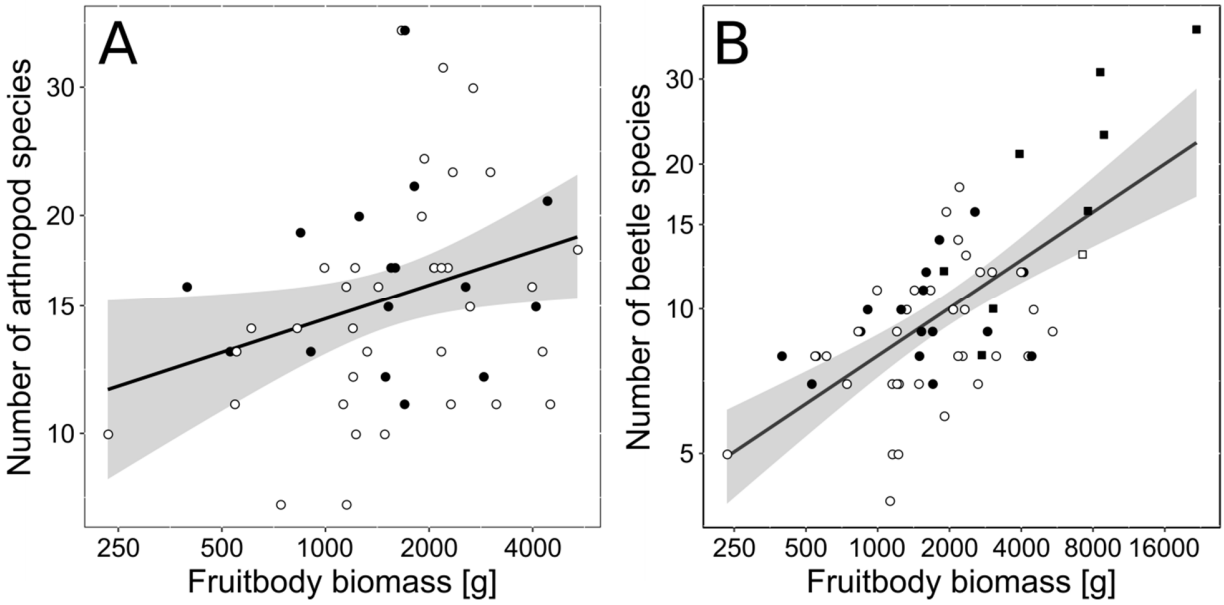

FIGURE 2.3.5. Relationship between (A) the number of arthropod species per fruitbody sample and sample size, i.e. the total weight of the 10 sporocarps sampled, of 52 sites and (B) the number of beetle species per fruitbody sample and sample size including all 61 sites. Circles indicate the 52 study sites for which data on all arthropods were available; squares indicate 9 sites for which only beetle data was available and which are part of the analyses in Appendix S4. Black filling indicates sites with active forest management, white filling indicates unmanaged sites. A simple regression line and confidence interval is shown. Axes are $\log_e$-transformed.

Our models for all beetle species explained up to 59 % of the deviance in alpha-diversity, 34 % in Sørensen dissimilarity and 19 % in Bray-Curtis dissimilarity (Tables 7.2.12, 7.2.13; Fig. 7.2.5). Variables linked to habitat amount consistently explained most of the deviance in models of species richness, overall community composition and community dissimilarity due to nestedness, while variables linked to spatial distance explained most of the deviance due to species turnover (Fig. 7.2.5).

Discussion

Overall, our results indicate that fruitbodies of *F. fomentarius* form an important micro-habitat in European beech forests, hosting a rich fauna (estimated ~ 600 arthropod species). However, the arthropod communities included about 30 dominant species which occurred at most sites across Europe and can be considered typical for fruitbodies of *F. fomentarius*. Moreover, there was a large number of species that use *F. fomentarius* fruitbodies occasionally. The latter group includes fungicolous species using a wider range of fungal hosts (e.g. *Bolitophagus interruptus,* Coleoptera, which is more common on *Ischnoderma* spp.), species that feed on white-rotten wood (e.g. *Corymbia scutellata*, Coleoptera) or fungal mycelia and species that use cavities inside fruitbodies simply for shelter (e.g. *Amaurobius fenestralis,* Aranaea) or that benefit from arthropod prey (e.g. *Plegaderus dissectus*, Coleoptera). Alpha-diversity increased with sample size and decreased with longitude, latitude and temperature. Despite the large extent covered in our study (approx. 1800 km in latitude and 3000 km in longitude) beta-diversity – which was characterized by high turnover – was not structured by drivers associated with space, the biogeography of F. sylvatica, and habitat amount. Moreover, increasing nestedness and decreasing alpha-diversity towards the east follows not the continental gradient of increasing

land-use intensity from the Carpathians to Western Europe.

Post-glacial dispersal lags have been identified as one of the driving mechanisms causing patterns of alpha- and beta-diversity across Europe in plants, insects and vertebrates (Svenning et al. 2008, 2011, Pinkert et al. 2018). In contrast, beta-diversity of saproxylic beetles was shown to be higher between sites than between elevational zones and bioregions (Müller et al. 2013). We found only a weak decrease in alpha-diversity of fungi specialists with latitude and no significant effect of latitudinal distance on beta-diversity of all arthropods and the trophic guilds in *F. fomentarius* fruitbodies. Only predatory species showed an increased rate in turnover with increasing latitudinal distance: the rate of change in species composition was highest at low latitudes (Table 7.2.7). There are several potential explanations as to why post-glacial recolonization of the main host tree species appears to be of minor relevance for communities of arthropods occurring in *F. fomentarius* fruitbodies. For instance, species associated with fungal fruitbodies in general display high dispersal abilities (Komonen and Müller 2018). Flight mill experiments showed a dispersal ability of *Neomida haemorrhoidalis* and *Bolitophagus reticulatus* (both Coleoptera; body length: 6 – 8 mm and 6 – 7.5 mm respectively; Wagner & Gosik 2016) of > 30 km and > 100 km, respectively (Jonsson 2003). Additionally, there is evidence that the genetic distance of fungivores does not increase with geographic distance, indicating the absence of dispersal limitation (Kobayashi and Sota 2016). Another possible explanation is that although European beech is the main host of *F. fomentarius* in temperate Europe today, other hosts that recolonized Europe much earlier – such as birch– are also frequently used (Judova et al. 2012). If *F. fomentarius* recolonized Europe with the latter tree species, its arthropods may have had more time for recolonization and thus post-glacial dispersal lags are less likely to be important. Last, if microrefugia of European beech also occurred in Central Europe (Robin et al. 2016), recolonization pathways may be complex and not well described by latitude used as a proxy for distance to major refugia in Southern Europe.

A gradient of decreasing anthropogenic pressure from Western to Eastern Europe explains why many specialist species of old-growth forests have become rare or extinct in Western Europe (Speight 1989, Ódor et al. 2006, Eckelt et al. 2018). We thus expected to find an increase of fungicolous arthropod alpha-diversity with increasing longitude, but in fact we observed a weak decrease. Additionally, we found a marginally significant increase in compositional dissimilarity due to nestedness with increasing longitudinal distance of the overall arthropod community. However, the rate of change in composition due to nestedness was highest at low longitudes, while explanatory power was low and nestedness did not account for more than 4% of compositional dissimilarity (Table 2.3.2). For beetles, we found an increased rate in turnover and balanced changes of abundance at the lower end of the longitudinal gradient (Tables 7.2.11, 7.2.12). In parallel to the gradient of historic anthropogenic pressure, there is an east-west climatic gradient from oceanic towards more continental climates, which is shown by a moderate correlation between climate variables and longitude (Table 7.2.5). Both, decreasing alpha-diversity and increasing nestedness with increasing longitude as well as increased beetle turnover at low longitudes is inconsistent with the expected effect of historic anthropogenic pressure, but

may also be explained by a milder climate in the west. However, we have to point out that we were not able to collect *F. fomentarius* samples in the westernmost regions (e.g. England) due to the rarity of fruitbodies of *F. fomentarius*. Moreover, many of our sites, also in Western Europe, were located in unmanaged forests (Fig. 2.3.1) and although forest management had no effect on overall community composition (Fig. 7.2.3), the gradient of anthropogenic pressure may be less pronounced across our sites than at a landscape scale.

Environmental filtering by climatic drivers is often an important mechanism structuring communities (Kraft et al. 2015, Cadotte and Tucker 2017), including dead-wood associated insects and fungi (Bässler et al. 2010a, Müller et al. 2013, Seibold et al. 2016). Being poikilothermic, arthropods generally benefit from higher temperatures (Schowalter 2006). However, we found a marginally significant negative effect of temperature on alpha-diversity. One possible explanation is that fruitbodies are drier and thus less suitable for some species in warmer climates. However, in general beta-diversity was not affected by dissimilarity in climatic conditions. This suggests that climate is of minor importance for arthropods associated with *F. fomentarius* despite considerable variability in climatic conditions within our sampling range (Fig. 2.3.1).

The amount of available habitat is one of the fundamental drivers of biodiversity (MacArthur and Wilson 1967, Fahrig 2013). In Europe, human activities over millennia have reduced the forests and features of old-growth stands (overmature and dead trees), which has led to a decline of many saproxylic insects (Seibold et al. 2015). Forest cover is only a coarse proxy for the amount of habitat available to species associated with dead wood or fruitbodies of *F. fomentarius*, as the amount of their actual habitat – dead wood or fruitbodies of *F. fomentarius*, respectively – can vary considerably within beech forests depending, e.g., on current forest management (Bässler et al. 2014, Abrego et al. 2015). This was also reflected by the time needed to find ten fruitbodies of *F. fomentarius* in the present study, which ranged from minutes to days. Nevertheless, we found the number of consumers among fungicolous arthropods and fungi specialists among beetles to increase with forest cover (700 m radius around sites). Consistent with results of earlier studies that found a positive effect of fruitbody availability on fungicolous beetle diversity at regional scales (Rukke 2000, Araujo et al. 2015) we found the number of arthropod species to increase with increasing fruitbody biomass. Although our measure of fruitbody biomass did not reflect the abundance of *F. fomentarius* at the sites, based on our results covering a range of fruitbody biomass from 0.4 to 21.7 kg and earlier findings at regional scales (Rukke 2000, Araujo et al. 2015), we expect more fungicolous arthropod species in forests with more fruitbodies of *F. fomentarius*.

For beetles, sample size strongly affected the number of species even when accounting for abundance, which suggests that habitat heterogeneity increases with fruitbody biomass (Table 7.2.9).

TABLE 2.3.2. Coefficients of three I-splines (i.e. 1, 2 and 3) from the GDM of overall beta-diversity, turnover and nestedness of all arthropod species. Significant ($P < 0.05$) or marginally significant ($P < 0.1$) *P*-values for the I-splines of the predictor variables after 999 permutations are given in bold. PC1 and PC2 refer to the first two axes of the respective principal component analyses of temperature or precipitation variables (see *Methods*).

Response matrix	Predictor set	Predictor	I-spline			Sum of coefficients	*P*
			1	2	3		
Overall beta	Space	Latitude	0.155	0.007	0.003	0.165	0.11
		Longitude	0	0.067	0	0.067	0.42
	Climate	Temperature (PC1)	0	0	0	0	0.99
		Temperature (PC2)	0.017	0	0	0.017	0.68
		Precipitation (PC1)	0	0	0	0	0.99
		Precipitation (PC2)	0.061	0	0	0.061	0.35
	Habitat amount	Forest cover	0	0.016	0	0.016	0.73
		Sample size	0.12	0	0	0.12	0.24
Turnover	Space	Latitude	0.116	0	0.054	0.170	0.24
		Longitude	0	0	0.082	0.082	0.46
	Climate	Temperature (PC1)	0	0	0	0	0.99
		Temperature (PC2)	0.004	0	0.030	0.034	0.65
		Precipitation (PC1)	0	0	0	0	0.99
		Precipitation (PC2)	0	0	0	0	0.99
	Habitat amount	Forest cover	0	0.018	0.001	0.019	0.73
		Sample size	0.121	0	0	0.121	0.25
Nestedness	Space	Latitude	0.001	0	0	0.001	0.70
		Longitude	**0.132**	**0**	**0**	**0.132**	**0.07**
	Climate	Temperature (PC1)	0.013	0	0	0.013	0.51
		Temperature (PC2)	0	0	0	0	0.98
		Precipitation (PC1)	0.010	0	0	0.010	0.57
		Precipitation (PC2)	0.018	0	0	0.018	0.47
	Habitat amount	Forest cover	0.05	0	0	0.05	0.27
		Sample size	0	0	0	0	0.97

Here, larger samples seem to provide more different habitat niches, e.g. through different stages of decomposition within and among fruitbodies (Dajoz et al. 1966) similarly as shown for coarse woody debris (Seibold et al. 2016). Concerning community composition, only the total beta-diversity and turnover component of predatory arthropods was affected by sample size. However, abundance-based dissimilarity in community composition of beetles was affected by longitude and sample size. Here, dissimilarity due to abundance gradients (analogous to nestedness) increased with sample size.

Overall, this indicates that local habitat amount is an important driver of alpha-diversity of fungicolous arthropod communities and, at least for fungicolous beetle communities, an important driver of beta-diversity.

Based on the ITS region, Judova et al. (2012) have suggested that populations of *F. fomentarius* are comprised of two sympatric cryptic species; this has been confirmed by Pristas et al.

(2013) using the efa gene. One genotype, termed genotype A, has been suggested to be prevalent on European beech while the other, termed genotype B, is additionally found on other host species (Judova et al. 2012). Our genetic analysis of *F. fomentarius* supports this, as all but 5 of 36 of our samples – all sampled from European beech – belonged to genotype A. Nevertheless, the occurrence of genotype B on European beech in the Pyrenees, southern Italy, Belgium and Denmark is a noteworthy result (see chapter 7.2). The low intraspecific variation among sites rendered an analysis of the inhabiting arthropod community based on genetic differences fruitless.

Further studies are needed to test the hypothesis that *F. fomentarius* of genotype B hosts arthropod communities different from genotype A.

In our analyses we incorporated variables which are known to be strong drivers of large-scale differences in community composition (Soininen et al. 2007, Dobrovolski et al. 2012, Zellweger et al. 2017). Furthermore, we accounted for differences in habitat specialization and trophic level, forest management intensity and biogeographic regions and even considered the genetic properties of the fruitbodies. Nevertheless, while our models explained considerable proportions of variation in alpha-diversity most of the variation in the community composition of arthropods occurring in fruitbodies of *F. fomentarius* remained unexplained. Although explaining the full variation in community composition was beyond the scope of this study, these results appear surprising. We suggest three directions for future studies. First, future studies investigating the community composition of arthropods occurring in fruitbodies of bracket-fungi should focus on factors driving community composition at local scales. This may include the amount of fruitbodies at the site and landscape scale which represent habitat availability and may affect population dynamics via increased dispersal success and rescue effects given sufficient patch connectivity (Venier and Fahrig 1996, Snäll and Jonsson 2001, Gonzalez 2005). Furthermore, studies could investigate the effects of microclimate as mediated by canopy openness and forest successional stage, which were shown to generate large differences in community composition in saproxylic organisms (Seibold et al. 2016, Hilmers et al. 2018b). Second, further studies need to include arthropod communities in fruitbodies of *F. fomentarius* on other host tree species, such as *Betula* spp. or *Populus* spp. and investigate potential alternative post-glacial recolonization routes. Third, to better understand scale-dependency of community turnover, future studies could cover the whole range of *F. fomentarius* including North America and East Asia. For instance, the Tenebrionidae *Bolitophagus reticulatus* is a ubiquitous species in *F. fomentarius* from Europe to Korea (Jung et al. 2007), but is completely replaced by its relative *Bolitotherus cornutus* in North America (Matthewman and Pielou 1971), indicating that there might be a stronger biogeographical structuring of the community at such larger scales.

Our results showed that fruitbodies of a single fungus *F. fomentarius* provide habitat to a high number of arthropods, thereby contributing considerably to biodiversity in European beech forests. Considering the responsibility of European countries to protect biodiversity in this ecosystem, we recommend making the promotion of bracket fungi as *F. fomentarius* an integrated goal of forest conservation strategies in European beech forests. The weak biogeographical structuring and high turnover of communities between sites suggests that a

prioritization of certain regions within Europe is of minor importance with regard to arthropod communities in *F. fomentarius*. Instead, we recommend that conservation should range from the protection of forests where *F. fomentarius* is highly abundant and inhabited by Europe-wide rare arthropod species (e.g. in the Carpathian Mountains), to the retention of individual habitat trees and dead wood with fruitbodies of the species from harvesting and salvage logging (including unintentional destruction by logging machinery) throughout Europe, and to the reintroduction of the species to regions (e.g. in Western Europe) where it has become extinct and relict populations are lacking (for methods see Abrego et al. 2016). The example of the region of Flanders, Belgium, shows that *F. fomentarius* is able to recolonize areas where it was formerly extinct from a few relict populations if beech dead wood and habitat trees are retained (Vandekerkhove et al. 2011). Furthermore, many fungicolous arthropods are able to track *F. fomentarius* populations recolonizing suitable habitats due to their high dispersal ability (Vandekerkhove et al. 2011; Zytynska et al. 2018). In addition to positive effects on species associated with its fruitbodies, promoting *F. fomentarius* will potentially help to restore fundamental ecosystem processes and natural forest dynamics in beech forests as it is the primary decomposer of beech wood and an important agent of tree senescence and death. Species associated with broadleaf dead wood and sunny conditions in forests may also benefit from gaps created when beech trees are killed by *F. fomentarius*. As *F. fomentarius* provides habitat, shapes further habitat characteristics and drives ecosystem processes, it can be considered a keystone modifier or ecosystem engineer in European beech forests (Mills et al. 1993).

Acknowledgments

We are grateful to all those who helped in the field and in the laboratory to conduct the study, Svitlana Los for providing samples from Crimea, Boris Büche for identification of beetles and Jérôme Morinière for lab support in DNA barcoding. We thank Emily Kilham for linguistic revision of the manuscript. Nicolas Friess received a scholarship from the Rudolf and Helene Glaser Foundation organized in the "Stifterverband für die deutsche Wissenschaft". M. Mikoláš and M. Svoboda were supported by the Czech University of Life Sciences, Prague (CIGA No. 20184304) and by the institutional project MSMT CZ.02.1.01/0.0/0.0/16_019/0000803.

Chapter 3.1

Habitat availability drives the distribution-abundance relationship in phytophagous true bugs in managed grasslands

with
Martin M. Gossner | Wolfgang W. Weisser | Roland Brandl | Martin Brändle

published in Ecology, 98 (10), 2017, p. 2561 – 2573

This paper is the follow-up to a pilot study I did during my B.Sc. studies. In the follow-up study, the conceptual framework was strongly developed, new data were collected, the analysis methodology completely revised and a new manuscript was written. Accordingly, this paper is a new scientific contribution to which I myself contributed the main part as lead author. For this chapter, there is a digital supplement with additional data on the enclosed compact disk.

Summary

The nearly universal positive relationship between the distribution and abundance of species has been explained by several hypotheses but hitherto no consensus has been reached. Here, we used monitoring data of 105 phytophagous true bug species (Heteroptera) from 150 grassland sites over six years, to test how (1) range-position, (2) resource-use, (3) resource-availability, (4) density-dependent habitat selection, (5) metapopulation dynamics and (6) habitat-dispersal affect the distribution-abundance relationship. For the use in a confirmatory path analysis, we constructed causal pathways representing the hypothesized relationships and tested them separately and in a combined analysis. Our results show that the distribution-abundance relationship in phytophagous true bugs is driven by habitat-availability. An increasing local density of the host-plants increases the distribution of the species in the landscape, which in turn increases their local abundance. Thereby habitat availability facilitates dispersal success. We conclude that local abundance of herbivores facing habitat destruction could decline owing to a decrease in population dynamics between sites at the landscape scale. Finally, our results underline the potential of confirmatory path analysis for testing competing hypotheses.

Introduction

The positive relationship between local abundance and spatial distribution of organisms is one of the classic patterns in macroecology (Hanski et al. 1993, Lawton 1999, Gaston et al. 2000, Holt et al. 2002, Blackburn et al. 2006, Borregaard and Rahbek 2010). This almost general relationship has been explained by several hypotheses, considering (i) range-position, (ii) resource-use, (iii) resource-availability, (iv) density-dependent habitat selection, (v) metapopulation dynamics and (vi) habitat-dispersal (Fig. 3.1.1a-f; Borregaard and Rahbek 2010).

The range-position hypothesis suggests that the observed relationship between distribution and abundance does not reflect an ecological process per se but rather represents a sampling bias. The abundance and occupancy of a species declines for several mutually non-exclusive reasons with increasing distance to the center of the distributional range (Brown 1984). This intraspecific spatial relationship can lead to a positive interspecific relationship between distribution and abundance, if the study area covers different parts of species' ranges. The range-position hypothesis predicts that the interspecific pattern will disappear when we control for differences in range-position of species (Fig. 3.1.1a; Gaston et al. 2000). From a statistical point of view, the significance of the interspecific distribution–abundance relationship may also be biased by phylogeny (Gaston et al. 1997b), because phylogenetically related species have similar traits (Harvey and Pagel 1991). Consider for example two closely related groups of species one with a low abundance and a restricted distribution and the other showing high abundance and a broad distribution. Across the two groups a positive relationship becomes apparent, even when there is no relationship among species within each group. However, the idea has received no empirical evidence and several studies have found a significant positive distribution–abundance relationship even after controlling for phylogenetic relatedness (Gaston et al. 1997a, Blackburn et al. 1997, Quinn et al. 1997).

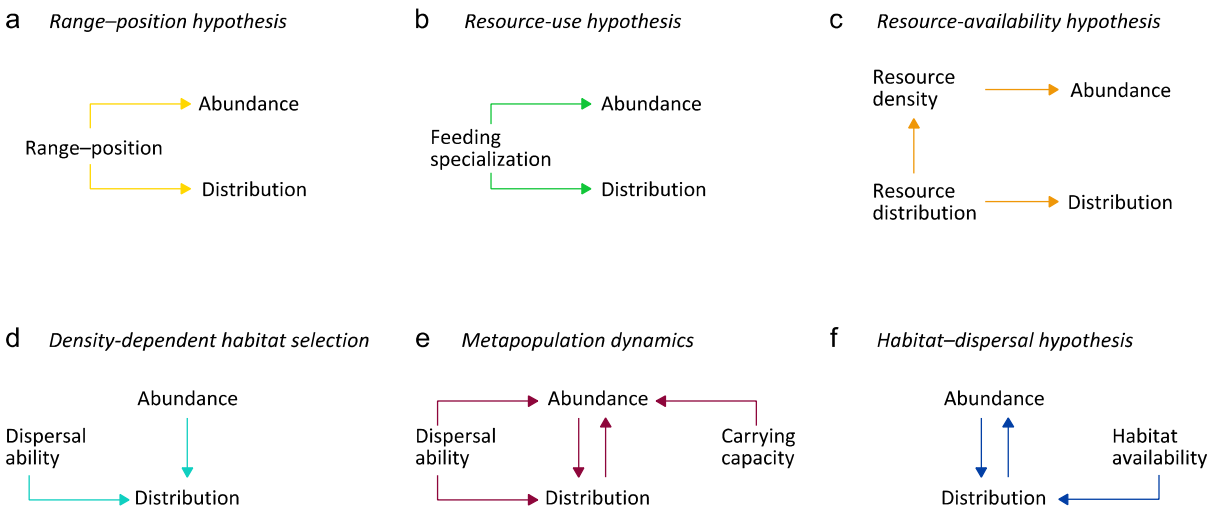

FIGURE 3.1.1. The causal pathways of the proposed explanations for the distribution-abundance relationship. Arrows indicate causal dependency. (a) The range-position hypothesis assumes that the distribution-abundance relationship vanishes when it is controlled for interspecific differences in range-position. (b) The resource-use hypothesis assumes that feeding specialization acts as a latent variable controlling distribution and abundance. (c) The resource-availability hypothesis assumes that the abundance of the resource controls species' abundances and the distribution of the resource controls species' distributions. The hypothesis assumes no causal link between distribution and abundance. (d) Density-dependent habitat selection assumes that high abundances and high dispersal abilities increase the distribution of a species. (e) Metapopulation dynamics assume that distribution and abundance affect each other over time and space due to population dynamics. The strength of the relationship is driven by the dispersal ability of a species. The abundance of a species is additionally affected by the carrying capacity of the sites a species occupies. (f) The habitat-dispersal hypothesis assumes that the probability for successful colonization of a site increases with the local habitat availability, while the relationship between distribution and abundance is driven by population dynamics independent of the dispersal ability of a species. Thus, species with higher local habitat availability should exhibit larger distributions on a landscape scale and subsequently increase in abundance. Please note, that these hypotheses are not mutually exclusive.

Other hypotheses explain the observed relationship with differences in ecological characteristics of the species and focus on the species' niche, specifically resource-use (Fig. 3.1.1b; Brown 1984) and resource-availability (Fig. 3.1.1c; Hutchinson 1957, Hanski et al. 1993). The resource-use hypothesis (Fig. 3.1.1b) proposes that species that utilize a broader spectrum of resources, e.g., an herbivorous insect feeding on several host plants, become both more widespread and abundant because of the higher probability of encountering a suitable resource in the landscape (Brown 1984, Kotze et al. 2003, Borregaard and Rahbek 2010).

This would lead to a broader distribution and a higher abundance of generalists compared to specialists. The resource-availability hypothesis (Fig. 3.1.1c) states that species utilizing abundant and widespread resources can attain high abundances and broad distributions themselves, leading to the positive distribution–abundance relationship (Hanski et al. 1993, Borregaard and Rahbek 2010). Of course, the resource-availability hypothesis and resource-use hypothesis are closely related, but each places the emphasis on different aspects of the resource: resource utilization and resource distribution. Nevertheless, both hypotheses do not assume a direct causal link between distribution and abundance and rather expect resource-use or –availability to act as a latent variable controlling both variables separately (Fig. 3.1.1 b-c). Consequently, these hypotheses do not predict a decrease in local abundance if species' distributions decrease and vice versa.

By contrast, other hypotheses assume direct causal links between local distribution and abundance and predict closely coupled dynamics between both variables (Fig. 3.1.1 d - f; Borregaard and Rahbek 2010). O'Connor (1987) proposed density-dependent habitat selection (Fig. 3.1.1d) as a potential mechanism that leads to a positive relationship between distribution and abundance. For species that reach high densities, some individuals will colonize low-quality habitats, thus leading to an increase in the regional distribution (cf. *ideal free distribution* (Fretwell and Lucas 1969)). Hence, the distribution is directly dependent on local abundance (Fig. 3.1.1d). This effect should be stronger for species with high dispersal abilities, which would lead to an independent positive effect of the propensity for dispersal on distribution (Fig. 1d). However, evidence for the importance of this mechanism is limited (but see: O'Connor 1987, Wiens et al. 1987, Marshall and Frank 1995).

A positive distribution–abundance relationship is also predicted by metapopulation models that incorporate carrying capacity and rescue effects (Hanski 1991, Nee et al. 1991, Gaston et al. 1997b). These models assume that the carrying capacities of habitats differ among species with some species being able to maintain larger local population sizes, which decreases their extinction probability and increases the number of colonizing individuals (Nee et al. 1991). Furthermore, rescue effects decrease the probability of local extinction with increasing immigration, which also leads to more occupied patches (Hanski 1991, Gyllenberg and Hanski 1992, Hanski et al. 1993, Hanski and Gyllenberg 1993). Focusing on this simple assumption, Gyllenberg and Hanski (1992) predicted that species with high dispersal rates should occupy more patches within a landscape than species that are less dispersive at the same levels of local abundance (Fig. 3.1.1e; Hanski et al. 1993). If resource-use or -availability affects the local carrying capacity of a species, we expect that this relationship will be stronger for generalists and for species with a high resource-availability, and thus lead to positive independent effects of resource-use or -availability on species' mean abundance (Fig. 3.1.1e).

In this context, Venier and Fahrig (1996, 1998) proposed a framework where the interplay of habitat availability and dispersal dynamics can generate a positive distribution–abundance relationship even if the assumptions of metapopulation models are false. This habitat–dispersal hypothesis (Fig. 3.1.1f) suggests that the dynamic mechanisms proposed by Gyllenberg and Hanski (1992) can lead to a positive distribution–abundance relationship independent of the dispersal ability of a species when dispersal success is determined by the amount of available habitat in a landscape (Venier and Fahrig 1996, 1998). The habitat–dispersal hypothesis thus assumes a dynamic causal interdependency of dispersal and abundance, but predicts that this relationship is independent of the propensity for dispersal of a species and rather assumes species' distributions to increase with local habitat amount (Fig. 3.1.1f). This relationship between habitat amount and species' distribution should be stronger for high-quality habitats than for low-quality habitats.

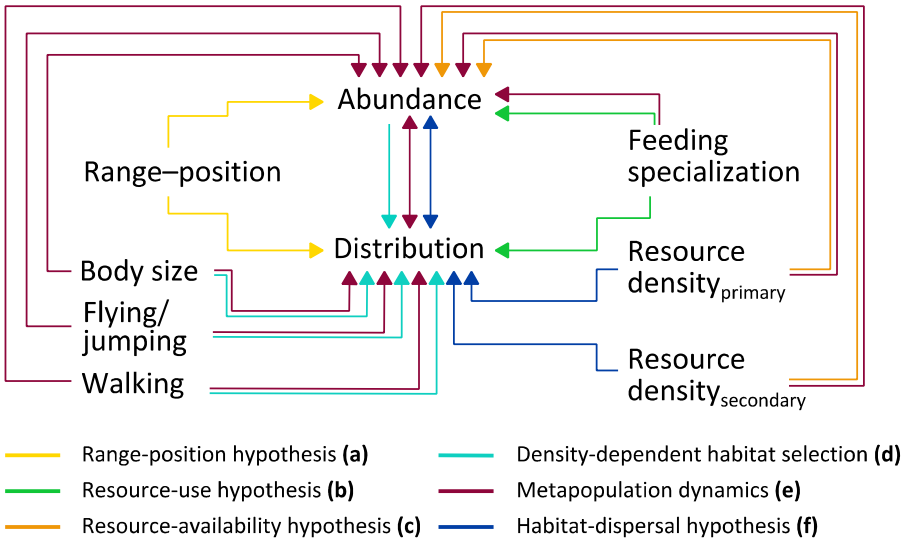

FIGURE 3.1.2. Conceptual framework for the confirmatory path analysis including all paths assumed by the different hypotheses. Arrow tips indicate causal direction. Differently colored arrows indicate the hypotheses as depicted in the legend in the lower part of the figure. The subscripts 'primary' and 'secondary' refer to the primary and secondary host-plants of the true bug species (see *Methods*). Please note, that these hypotheses are not mutually exclusive.

In the present study, we analyzed the distribution–abundance relationship of phytophagous true bug species (Heteroptera) sampled in a long-term monitoring project in managed grasslands located in three regions of Germany. Herbivorous true bugs are a comparatively species-rich insect taxon in grasslands (Morris 1979). They vary considerably in local abundance and range from monophagous species that feed on only one host plant (e.g., *Catoplatus fabricii*, Tingidae; host plant *Leucanthemum vulgare*) to polyphagous species that feed on a wide range of host plants (e.g. *Lygus rugulipennis*, Miridae; known to feed on ca. 400 plant species of 5 families). Furthermore, the host plants of herbivorous true bugs in Central Europe are comparatively well known, which allows us to test hypotheses related to the resource and habitat availability of the species.

We expected that true bugs will show a positive distribution–abundance relationship as previously shown for numerous other insect taxa (Borregaard and Rahbek 2010). We analyzed the relationship considering the distinct causal relationships predicted by the abovementioned six hypotheses (Fig. 3.1.1a-f). Since these hypotheses need not be mutually exclusive we tested each of the hypotheses separately (Fig. 3.1.1), as well as in a combined framework including all causal pathways predicted by the hypotheses (Fig. 3.1.2).

Methods

Study area

Our study was conducted within the *Biodiversity Exploratories* (for detailed information see Fischer et al. 2010). In this project, three exploratories were established for long-term research. The exploratories are situated in three geographic regions of Germany, namely the UNESCO Biosphere Reserve Schwäbische Alb (Swabian Jura, 48°20´28´´ – 48°32´02´´N / 9°10´49´´ – 09°35´54´´E, ~ 422 km², 460–860 m a.s.l.), the UNESCO Biosphere Reserve Schorfheide-Chorin (52°47´25´´ –

53°13´26´´N / 13°23´27´´ – 14°08'53"E, ~ 1300 km², 3–140 m a.s.l.), and the National Park Hainich and surrounding Dün-region (50°56´14´´ – 51°22´43´´N / 10°10´24´´ – 10°46´45´´E, ~ 1300 km², 285–550 m a.s.l.). In each region, experimental plots (50 m x 50 m) within a larger grassland site were chosen from a total of 500 candidate sites (100 m x 100 m grid) by stratified random sampling. This was done to minimize confounding factors such as spatial position or soil type and ensured that the plots covered the whole range of management types of the region. Minimum distance between grassland sites was 200 m. Each grassland site is located within a larger management unit (mean ± SE: 94 ± 10 ha, range: 5 – 800 ha) of a grassland complex, which has a history of broadly similar land-use intensity.

True bug abundance and local distribution

The relative abundance of true bugs was assessed between 2008 and 2013 using standardized sweep netting (a total of 60 double sweeps along three 50 m plot border transects of each experimental plot within a larger grassland site). True bugs were sampled during dry periods in June and August (Simons et al. 2014, 2015). We considered only herbivorous species that utilize herbaceous plants and shrub species as main food resource; omnivorous species that use plant and animal food resources at about equal proportions were excluded. We excluded soil living species because sweep netting is likely to underestimate species abundance. Furthermore, we excluded also species restricted to trees because these species occur only accidently in grasslands. The distribution of a species within each exploratory was estimated according to the proportion of occupied plots during at least one year of the sampling period. The mean abundance of a species across plots of each exploratory was estimated by dividing the total number of sampled individuals over the six sampling years by the number of occupied plots and is therefore a measure for the density of a species. We included 105 species (Alb: n = 77, Hainich: n = 69 and Schorfheide: n = 64) in our analyses. For statistical analyses, the mean abundance was $\log_e$-transformed and the local distribution was logit-transformed (Borregaard and Rahbek 2010).

Range–position

Based on data from the literature, we generated distribution maps for each species for the Palearctic and calculated the centroid of the range (Fig. 8.1.1; Digital Supplementary). Afterwards we calculated the distances between the centroid and the three regions using the haversine formula (Sinnott 1984). Since the distance to the centroid of the range is a function of the range size, we used the residuals of the linear relationship between the two variables as a corrected measure for the range–position (Fig. S8.1.2).

Propensity for dispersal

Since no reliable measures for dispersal rates for true bugs are currently available, we used already published morphological data as indicators for the propensity of dispersal (Gossner et al. 2015b). Morphological traits are often highly correlated with dispersal ability; however, results should be interpreted with caution (Sekar 2012). For all considered true bug species, we included body volume (i.e., as biovolume: body length × body width × body height; Siemann et al. 1999), hind femur length, hind femur width and, wing length as morphometric traits most likely linked to the propensity of dispersal (Clobert et al. 2012). Morphometric measures show allometric relationships; therefore, we performed a principal component analysis on

the covariance matrix of the $\log_e$-transformed measures to obtain uncorrelated estimates. We extracted three principal components using the rda function implemented in the vegan package (Oksanen et al. 2015). In the following we will use the terms body size, flying/jumping ability and walking ability to refer to the three extracted components (for details see chapter 8.1). For body size, larger values indicate larger-bodied species; for flying/jumping ability, larger values indicate better flying and jumping abilities; and for walking ability, larger values indicate better walking abilities.

Resource-use

Information on the host plant utilization mode was derived from a published dataset (Gossner et al. 2015a). From these data, we classified species as monophages, i.e., species feeding on plant species of one genus (14 of 105 species); oligophages. i.e., species feeding on plants of one higher lineage (55 of 105 species), specifically bryophytes, ferns, gymnosperms, angiosperms: monocots, angiosperms/ basal eudicots, angiosperms/ eurosids, and angiosperms/ euasterids; and polyphages, i.e., species feeding on plants of more than one higher lineage (36 of 105 species; Gossner et al. 2015a). Although the variable measuring the breadth of host use has only three ordered values we considered the variable to be continuous ranging from 1 (polyphagous) to 3 (monophagous).

Resource-availability

Information on distribution and abundance of potential host plants based on vegetation relevés (ground cover estimation to the nearest percent on 4 m × 4 m, following Wisskirchen and Haeupler, 1998) was extracted from annual field surveys in the Biodiversity Exploratories (Socher et al. 2012, 2013). The corresponding host plants of the true bug species were derived from the literature (see chapter 8.1 and Digital Supplementary). We considered measures of resource-density and resource occupancy in our analysis. Resource occupancy refers to the proportion of sites in which at least one host plant occurred in at least one year between 2008 and 2013. Resource density refers to the mean ground cover of the potential host plants across the years 2008 to 2013 on sites where the true bug species occurred. For statistical analyses, resource densities were $\log_e$-transformed and resource occupancies were logit-transformed. All measures were separately calculated for primary host plants of a species (in the following indicated by the subscript *primary*) and for secondary host plants (host plants that are exploited only occasionally; in the following indicated by the subscript *secondary*), as categorized in the literature. This is necessary, since information on secondary host-plants is often very vague and frequently only available on a genus or family level and therefore might lead to an overestimation of the habitat availability of the species. Primary host-plants better represent the crucial habitat of the species, in the sense that these species are utilized as a feeding source but also more likely as a breeding ground and for oviposition. Secondary host plants are less frequently used by a particular species and mostly by adults. Thus, the density of primary host-plants offers better representations of the overall habitat of the species as assumed by the hypotheses linked to metapopulation dynamics and habitat-dispersal.

Confounding effect of land-use intensity

A previous study in our study regions indicated that land-use intensity of managed grasslands affects the shape of species abundance distributions of arthropods (Simons et al. 2015). With

high land-use intensities, rare species tend to become rarer, while the most abundant species become more dominant. Since our study sites exhibit a gradient in land-use intensity, we also considered land-use intensity as a confounding factor of the abundance patterns of species. For our study sites, information is available on the management intensities estimated by a composite land-use intensity index (for details see Blüthgen et al. 2012). Briefly, this index sums for each site the intensity of mowing, grazing, and fertilization into a continuous, regionally standardized value. We calculated the mean land-use intensity index for 2006–2013 for the sites occupied by a true bug species, as the species niche position along the land-use gradient. We tested for the effect of the mean land-use intensity on distribution and abundance separately and in the combined framework. Since, land-use intensity had no significant effect on distribution or abundance in both analyses we excluded the variable in the main analysis (Table 8.1.5). This was additionally based on the fact, that there is currently no established hypothesis in the literature linking land-use intensity to the distribution-abundance relationship.

Statistical analyses

All statistical analyses were performed using the statistical software R, version 3.00.0 (R Core Team 2013). Our final dataset included information on 105 true bug species on 150 sites for 2008–2013 (for the full species list, see Digital Supplementary). The probability distributions of the variables were checked and transformed when necessary to meet the assumptions of the statistical tests applied (Table 8.1.2). The relationship between mean abundance ($\log_e$-transformed) and local distribution (logit-transformed) was tested via linear regression for each exploratory. The outlined hypotheses make distinct predictions on the causal relationships among the variables (Fig. 3.1.1). We formulated structural equations representing the predictions for each hypothesis separately in order to test for the likelihood of each piecewise structural equation model (Table 3.1.1). All variables were centered and scaled in order to get comparable parameter estimates. The structural equations were formulated as linear mixed models using the lmer function implemented in the R-package lme4 (Bates et al. 2013). For each predictor variable we calculated the variance inflation factor using a slightly modified version of the vif function implemented in the R-package car (Fox and Weisberg 2011). Following the recommendations of Zuur et al. (2010) predictor variables with a variance inflation factor > 2 were considered to cause multicollinearity effects and were subsequently dropped from the model in order to evaluate how their inclusion affects the parameter estimates. In the mixed models we included the genus and the species identity as a nested random effect. With genus and species identity as a nested random effect, we can account for introduced extra-variance by non-independent differences among genera and species, such as phylogenetic relatedness, and the replication of species among the threes study regions (Harrison 2014). In order to test the hypothesis linked to metapopulation dynamics we included a link from the feeding specialization, as well as the host-plant densities on the mean abundance of the species, representing the carrying capacity of a site (Fig. 3.1.1e; Table 3.1.1). As an estimate for the local habitat availability in the context of the habitat-dispersal hypothesis, we included a link from the host-plant densities on the distribution of the species (Fig. 3.1.1f; Table 3.1.1). In this context the densities of primary and secondary host-plants represent the amount of high- and low-quality habitats, respectively. Since the outlined hypotheses

need not be mutually exclusive we additionally formulated a model of structural equations including all hypotheses (Fig. 3.1.2; Table 3.1.1). Due to the obvious collinearity among the variables resource density and resource distribution we only included resource density in the model of the combined framework (Table 3.1.1). The dependency claims of each model were tested for statistical support using Shipley's test of d-separation for piecewise structural equation models as implemented in the piecewiseSEM package (Shipley 2009, 2013, Lefcheck 2015). The models of each hypothesis were then compared by their goodness-of-fit using AIC_C and the chi-square test on Fischer's *C* (Shipley 2013). All models were tested once considering and once omitting polyphagous true bug species to test for consistency, taking into consideration that the information on the host plants of polyphagous species is less likely to be reliable compared to information available for monophages and oligophages.

Results

In all three study regions, we found a strong positive, bivariate relationship between mean abundance and local distribution (Alb: r^2 = 0.74, $P < 0.001$; Hainich: r^2 = 0.68, $P < 0.001$; Schorfheide: r^2 = 0.74, $P < 0.001$; Fig. 3.1.3). All six hypotheses were tested with piecewise structural equation models representing their causal structure outlined in Fig. 3.1.1 and 3.1.2:

Model a. —Concerning the range-position hypothesis we did not find an effect of species' range-position on its mean abundance or local distribution (Table 3.1.1; Fig.3.1.4a) and the model consequently had no statistical support based on the chi-square test on Fisher's *C* (*C* = 193.7, df = 2, $P < 0.001$; Table 3.1.1).

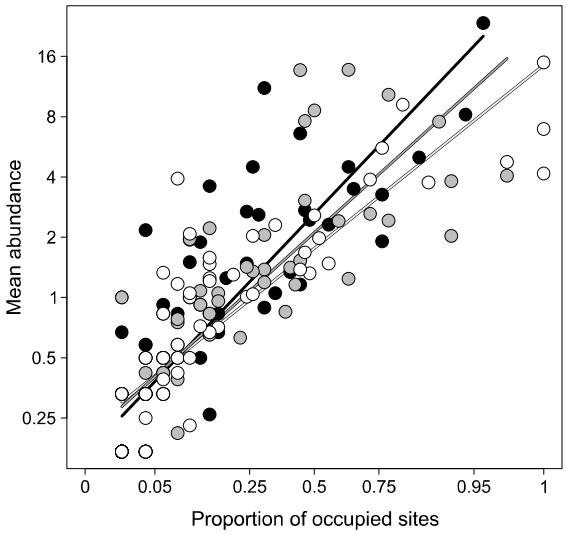

FIGURE 3.1.3. The positive relationship between mean abundance and the proportion of occupied sites for true bug species in the three regions Schwäbische Alb (black filled circles and line; linear model: $r^2 = 0.74$, $P < 0.001$, n = 77), Hainich (gray filled circles and line; linear model: $r^2 = 0.68$, $P < 0.001$, n = 69) and Schorfheide-Chorin (open circles and line; linear model: $r^2 = 0.74$, $P < 0.001$, n = 64). Note that mean abundance was $\log_e$-transformed and the proportion of occupied sites was logit-transformed.

Model b. —Concerning the resource-use hypothesis species' feeding specialization did not affect its mean abundance and local distribution (Table 3.1.2; Fig. 3.1.4b) and thus the model was not supported (*C* = 205.0, df = 2, $P < 0.001$; Table 3.1.1).

Model c. —Concerning the resource availability hypothesis we found significant positive effects of resource distribution on resource density, as well of resource density on species' mean abundance and of resource distribution on species' local distribution (Table 3.1.2; Fig. 3.1.4c). The overall model was however not statistically supported (*C* = 377.6, df = 16, $P < 0.001$).

Model d. —Concerning the hypothesis related to density dependent habitat selection we found a highly significant positive effect of species' mean abundance on its local distribution and a

weak positive effect of walking ability on species' distribution, but no significant effects of body size and flying/jumping ability on species' local distribution (Table 3.1.2; Fig. 3.1.4d). Since, this hypothesis could not be modeled as an acyclic path diagram we could not perform a test on Fisher's *C*. In comparison to the other models we found a very high AIC_C-value suggesting a weak fit (Table 3.1.1).

TABLE 3.1.1. Structural equations used in the piecewise structural equation models.

Model and response	Structural equations	R^2_M	R^2_C	*C*	df	*P*	AIC_C	K
a								
Abundance	~range position	<0.01	0.66	205.7	2	<	226.8	10
Distribution	~range position	0.02	0.70			0.001		
b								
Abundance	~feeding specialization	<0.01	0.67	205.0	2	<	226.2	10
Distribution	~feeding specialization	0.01	0.71			0.001		
c								
Abundance	~resource density$_{primary}$ + resource density$_{secondary}$	0.56	0.78	377.6	16	<	427.0	22
Distribution	~resource distribution$_{primary}$ + resource distribution$_{secondary}$	0.18	0.73			0.001		
Resource density$_{primary}$	~resource distribution$_{primary}$	0.40	0.83					
Resource density$_{secondary}$	~resource distribution$_{secondary}$	0.58	0.90					
d								
Distribution	~abundance + body size + flying/jumping ability + walking ability	0.70	0.86	-	-	-	311.7	-
e								
Abundance	~distribution + resource density$_{primary}$ + resource density$_{secondary}$ body size + flying/jumping ability + walking ability + feeding specialization	0.73	0.84	87.3	6	< 0.001	129.3	19
Distribution	~abundance + body size + flying/jumping ability + walking ability	0.70	0.86					
f								
Abundance	~distribution	0.72	0.84	8.5	4	0.08	34.1	12
Distribution	~resource density$_{primary}$ + resource density$_{secondary}$	0.80	0.91					
All								
Abundance	~distribution + body size + flying/jumping ability + walking ability + feeding specialization + resource density$_{secondary}$ + range position	0.72	0.84	3.4	2	0.18	55.4	23
Distribution	~abundance + body size + flying/jumping ability + walking ability + feeding specialization + resource density$_{primary}$ + resource density$_{secondary}$ + range position	0.81	0.91					

Notes: Model refers to the corresponding hypotheses in Fig. 3.1.1 and 3.1.2. All models included genus and species identity as a nested random factor. The related hypotheses are as follows, (a) range-position hypothesis, (b) resource-use hypothesis, (c) resource-availability hypothesis, (d) density-dependent habitat selection, (e) metapopulation dynamics, (f) habitat-dispersal hypothesis and (all) all hypotheses combined (Fig. 3.1.5). Reported statistics include marginal R^2 (R^2_M), conditional R^2 (R^2_C), Fisher's *C*, the chi-squared test degrees of freedom (df), *P*-value of the Chi-squared significance test, AIC_C value (AIC_C) and the likelihood degrees of freedom (*K*). Note that model (d) is based on a regular linear mixed effect model and thus the statistics for piecewise structural equation models are not available (see *Results*). The subscript 'primary' and 'secondary' refers to primary and secondary host-plants (see *Methods*).

TABLE 3.1.2. Results from the piecewise structural equation modelling, including standardized effect sizes (SES), standard errors (SE), *P*-values (*P*) and the variance inflation factor (VIF).

Model and response	Predictor	SES	SE	P	VIF
a					
Mean abundance	range-position	-0.10	0.08	0.18	1.00
Local distribution	range-position	-0.04	0.08	0.63	1.00
b					
Mean abundance	feeding specialization	-0.06	0.08	0.51	1.00
Local distribution	feeding specialization	-0.09	0.08	0.27	1.00
c					
Mean abundance	**resource density$_{primary}$**	**0.66**	**0.06**	**< 0.001**	**1.16**
Mean abundance	**resource density$_{secondary}$**	**0.21**	**0.06**	**< 0.01**	**1.16**
Local distribution	**resource distribution$_{primary}$**	**0.34**	**0.06**	**< 0.001**	**1.03**
Local distribution	resource distribution$_{secondary}$	0.09	0.07	0.23	1.03
Resource density$_{primary}$	**resource distribution$_{primary}$**	**0.53**	**0.05**	**< 0.001**	**1.00**
Resource density$_{secondary}$	**resource distribution$_{secondary}$**	**0.68**	**0.05**	**< 0.001**	**1.00**
d					
Local distribution	**mean abundance**	**0.70**	**0.05**	**< 0.001**	**1.10**
Local distribution	body size	0.08	0.04	0.10	1.03
Local distribution	flying/jumping ability	0.01	0.05	0.77	1.01
Local distribution	**walking ability**	**0.10**	**0.05**	**0.06**	**1.08**
e					
Mean abundance	**local distribution**	**0.73**	**0.07**	**< 0.001**	**3.02**
Mean abundance	resource density$_{primary}$	0.11	0.08	0.17	2.93
Mean abundance	resource density$_{secondary}$	0.09	0.05	0.11	1.28
Mean abundance	feeding specialization	0.02	0.05	0.71	1.17
Mean abundance	body size	-0.02	0.05	0.65	1.24
Mean abundance	flying/jumping ability	-0.03	0.05	0.47	1.01
Mean abundance	walking ability	0.03	0.05	0.54	1.18
Local distribution	**mean abundance**	**0.70**	**0.04**	**< 0.001**	**1.10**
Local distribution	body size	0.08	0.05	0.10	1.03
Local distribution	flying/jumping ability	0.01	0.05	0.77	1.01
Local distribution	walking ability	**0.10**	**0.05**	**0.06**	**1.08**
f					
Mean abundance	**local distribution**	**0.85**	**0.04**	**< 0.001**	**1.00**
Local distribution	**mean abundance**	**0.43**	**0.04**	**< 0.001**	**1.89**
Local distribution	**resource density$_{primary}$**	**0.45**	**0.05**	**< 0.001**	**1.82**
Local distribution	**resource density$_{secondary}$**	**0.11**	**0.04**	**< 0.01**	**1.18**
All					
Mean abundance	**local distribution**	**0.81**	**0.05**	**< 0.001**	**1.35**
Mean abundance	range-position	0.04	0.05	0.41	1.19
Mean abundance	feeding specialization	-0.01	0.05	0.96	1.24
Mean abundance	resource density$_{secondary}$	0.09	0.05	0.09	1.30
Mean abundance	body size	-0.01	0.05	0.91	1.19
Mean abundance	flying/jumping ability	-0.03	0.05	0.52	1.04
Mean abundance	walking ability	0.03	0.05	0.54	1.18
Local distribution	**mean abundance**	**0.43**	**0.04**	**< 0.001**	**1.88**
Local distribution	range-position	-0.05	0.04	0.19	1.14
Local distribution	feeding specialization	0.02	0.04	0.71	1.23
Local distribution	**resource density$_{primary}$**	**0.47**	**0.05**	**< 0.001**	**1.91**
Local distribution	**resource density$_{secondary}$**	**0.10**	**0.05**	**< 0.05**	**1.26**
Local distribution	body size	-0.05	0.05	0.24	1.22
Local distribution	flying/jumping ability	0.02	0.04	0.58	1.03
Local distribution	walking ability	0.07	0.04	0.12	1.12

Notes. Lower case letter in the column model corresponds to the structural equations in Table 3.1.1 and the path diagrams in Figures 3.1.4 and 3.1.5. Significant effects are in bold. The subscript 'primary' and 'secondary' refers to primary and secondary host-plants (see *Method*).

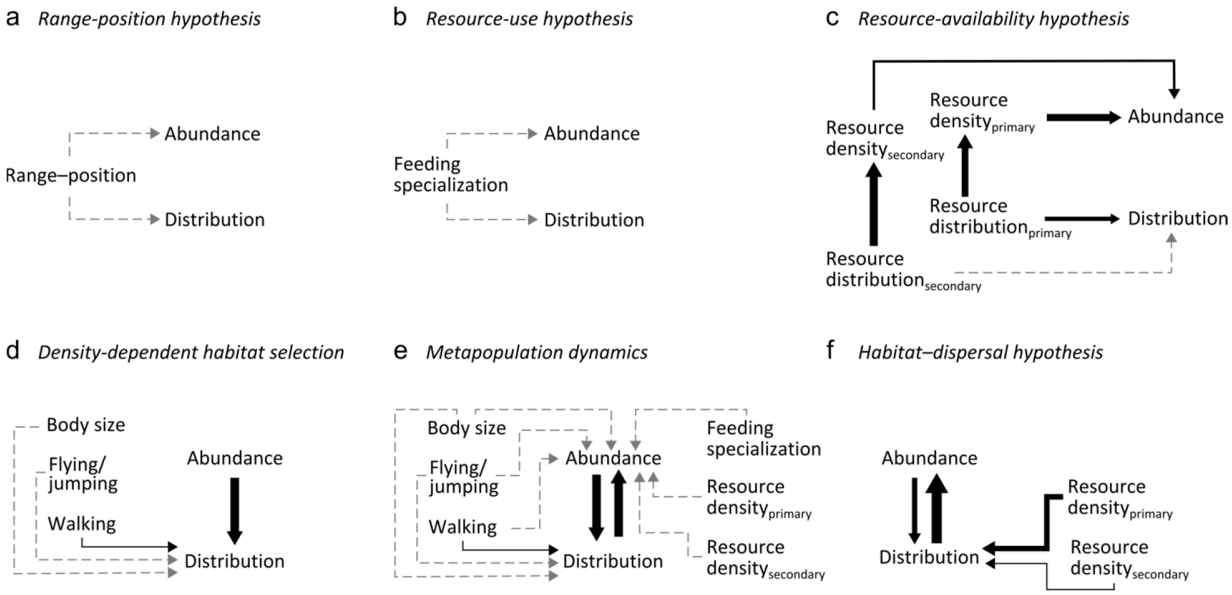

FIGURE 3.1.4. Results of the piecewise structural equation models separately for each hypothesis. Bold arrows indicate significant effects, dashed arrows indicate non-significant effects. Arrow thickness is adjusted according to the standardized effect size (Table 3.1.2). The subscripts '*primary*' and '*secondary*' refer to the primary and secondary host-plants of the true bug species (see *Methods*).

Model e. —Concerning the hypothesis representing metapopulation dynamics we found significant effects of species' mean abundance and local distribution on the respective other. Resource density and species' feeding specialization, representing the carrying capacity the species encountered on the sites, had no significant effect on species' mean abundance. The variables linked to species' dispersal propensity had no significant effect on its mean abundance or local distribution except for a weak positive effect of the walking ability on species' distribution (Fig. 3.1.4e; Table 3.1.2). The overall model, however was not supported according to the chi-square test on Fisher's *C* (C= 87.3, df = 6, $P < 0.001$; Table 3.1.1). In this model the variance inflation factors of species' local distribution and resource density of the primary host-plants exceeded the critical value of 2. Thus, we calculated the model again excluding the resource density of the primary host-plant. The variance inflation factor of species' local distribution decreased with the removal of resource density, indicating collinearity between these two variables as confirmed below. The removal however, did not change the result that the overall model was not supported (C = 12.9, df = 4, $P < 0.05$).

Model f. —Concerning the model representing the habitat-dispersal hypothesis we found significant positive effects of species' mean abundance and local distribution on the respective other. Furthermore, we found significant positive effects of resource densities of primary and secondary host-plants on the species' local distribution. Here, we found the greatest effect size from the density of the primary host-plant on species' local distribution. This effect was even stronger than the one from species' mean abundance on its local distribution. Notably, the model revealed a much stronger effect from species' local distribution on its mean abundance, than the other way around (Table 3.1.2; Fig. 3.1.4f). Here, the overall model was

statistically supported (C =8.5, df = 4, P = 0.08; Table 3.1.1).

Comparing the AIC_C-values of the six models revealed that the model representing the habitat-dispersal hypothesis (model f) performed best by several magnitudes and was the only model that was supported according to Fishers' C (Table 3.1.1). The model including all causal pathways in a combined framework predicted by the six hypotheses revealed significant effects from mean abundance and local distribution on the respective other, as well as significant positive effects of the resource densities of the primary and secondary host-plants on the local distribution (Fig. 3.1.5; Table 3.1.2). As already shown for the model representing the habitat-dispersal hypothesis (Fig. 3.1.4f), the effect of distribution on abundance was much higher than the effect of abundance on distribution and the effect of the density of the primary host-plants on distribution was stronger than the effect of mean abundance (Table 3.1.2). All other paths were not significant. The overall model was statistically supported (C = 3.4, df = 2, P = 0.18). It has to be considered that we had to remove the path from resource density of the primary host-plants to mean abundance, due to its variance inflation factor exceeding a value of 2. The test for the significance of the independence claims showed however, that the path was not significant and hence justified its removal (SES = 0.11, SE = 0.08, P = 0.18). Removing all non-significant pathways from the model resulted in the model representing the habitat-dispersal hypothesis. The results of our analysis remained consistent when polyphagous species were excluded from the analysis (Tables 8.1.3 and 8.1.4).

Discussion

In our study, the best model (model f; Fig. 3.1.1, 3.1.2, 3.1.4) revealed two important relationships (1) a strong effect of the density of the primary host-plant on species' distribution and (2) the effect of distribution on abundance exceeding the effect of abundance on distribution. This suggests a mechanistic link from high habitat availabilities to broad distributions, which in turn leads to high local abundances. High abundances then feed back into higher distributions most probably by population dynamics among sites. Overall our results appear to be robust and reliable for several reasons; first, they were consistent when polyphagous species were removed from the analysis. Second, by including the genus and the species identity as a nested random effect in our analyses we accounted for similarities among species originating in the phylogenetic relatedness (Blackburn and Duncan 2001, Bolker et al. 2009). Third, we found low values of the variance inflation factor for the variables, indicating that our models are not affected by multicollinearity effect. To our knowledge, no published study is available that compared several hypotheses aiming to explain the distribution–abundance relationship simultaneously in a framework including causal relationships (Borregaard and Rahbek 2010). Before drawing major conclusions from our study, we will discuss why other hypotheses outlined in the introduction might not apply in our study system and do not account for the distribution–abundance relationship.

The range–position hypothesis (Fig. 3.1.1a) proposes that a relationship of distribution and abundance might arise because the abundance of species and the number of occupied sites decline from the center to the border of the distributional range (Brown 1984). Interspecific differences in species' distances to the center of

their distributional range could then lead to a positive distribution–abundance relationship. We found no evidence for an effect of the range–position of species on the mean abundance or local distribution in our system. Grasslands in Central Europe almost always originated from human land use, which might have generated a sufficient number of suitable habitat patches even at the edge of the range of a species. This implies that the range–position hypothesis might apply only for systems with little or no human impact.

Empirical evidence for the resource-use hypothesis (Fig. 3.1.1b) is weak and ambiguous (Gaston et al. 1997b; positive relationships: e.g. Barger and Esch 2002, Kotze et al. 2003, Heino 2005, Faulks et al. 2015; no relationship: Gaston and Lawton 1988, Root and Cappuccino 1992, Gregory and Gaston 2000, McCreadie and Adler 2014; negative relationships: Gaston et al. 1997b, Päivinen et al. 2005, Verberk et al. 2010). In our study, the degree of feeding specialization had no effect on either the local distribution or the mean abundance of a species. This suggests that there are not necessarily more resources available for generalists than for specialists on a regional scale (Venier and Fahrig 1996) or at least not in such a way that its effect could drive the relationship of distribution and abundance. The resource-availability hypothesis (Fig. 3.1.1c) assumes that species utilizing widespread and abundant resources become themselves widespread and abundant (Gaston et al. 1997b, Borregaard and Rahbek 2010). The resource-availability is closely linked to the niche–position of a species and the hypothesis has received some empirical support for various taxa, including stream insects (Heino 2005, but see: McCreadie and Adler 2014), fish (Tales et al. 2004) and birds (Gregory and Gaston 2000).

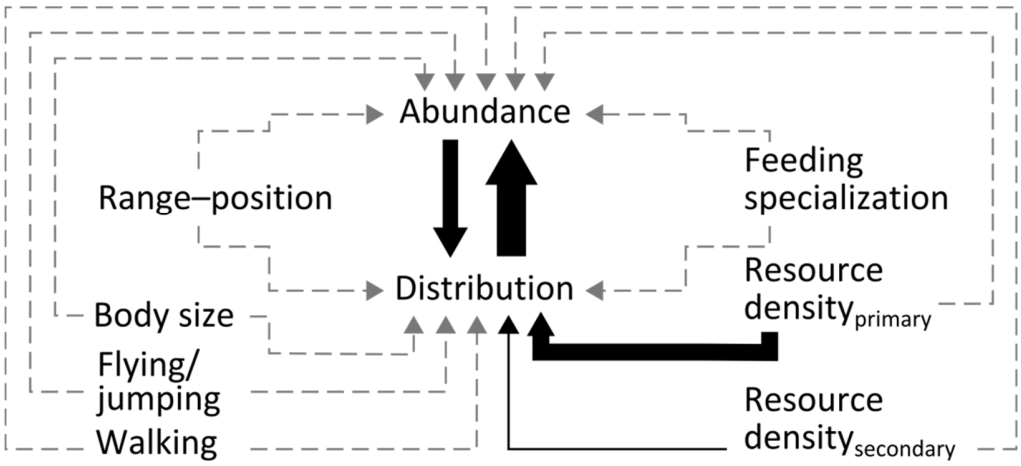

FIGURE 3.1.5. Results of the piecewise structural equation model including the paths of all hypotheses as depicted in fig. 3.1.2. Bold arrows indicate significant effects, dashed arrows indicate non-significant effects. Arrow thickness is adjusted according to the standardized effect size (Table 3.1.2). The subscripts '*primary*' and '*secondary*' refer to the primary and secondary host-plants of the true bug species (see *Methods*).

However, so far no study has shown that resource-availability alone can generate the distribution–abundance relationship (Borregaard and Rahbek 2010). In our study we found positive effects of resource density on the abundance of true bug species, as well as positive effects of host-plant distribution on the species' distribution. However, the overall model was not supported and it turns out, that rather host-plant density affects the distribution of phytophages than their abundances. This instance might as well be overlooked when hypotheses are tested by linear models that do not test for the significance of the independence claims. This underlines the strength of the confirmatory path analysis approach.

Empirical support has been found for positive density-dependent habitat selection (Fig. 3.1.1d) for some taxa, including passerine birds (O'Connor 1987) and fish (Marshall and Frank 1995, Blanchard et al. 2005). Positive density-dependent habitat selection assumes a causal dependency from distribution on the abundance of the species mediated by their propensity for dispersal. Our results show a positive effect of mean abundance on species' distribution; however morphological measures linked to the propensity of dispersal had no significant effect on mean abundance or local distribution and the model was not supported. Additionally, in the combined framework our model revealed a greater effect of distribution on abundance than vice versa, thus rendering it unlikely that density-dependent habitat selection alone shapes the distribution–abundance relationship for grassland true bugs.

Metapopulation dynamics models (Fig. 3.1.1e) predict a positive independent effect of dispersal ability on distribution or abundance or both, while the relationship between distribution and abundance persists (Hanski et al. 1993, Hanski 1999, Borregaard and Rahbek 2010). Furthermore, abundance is expected to be positively affected by the carrying capacity of the sites a species colonizes, which we assumed increases with local host-plant density and decreases with species' feeding specialization. Metapopulations are formed in landscapes with isolated habitat patches, frequent extinctions of local populations, and colonization of empty habitats. There is some evidence for metapopulation dynamics shaping the relationship for some taxa, including microarthropods inhabiting mosses (Gonzalez et al. 1998), rock-pool *Daphnia* (Östman 2010) and aquatic plants (Riis and Sand-Jensen 2002). However, it has been questioned whether most taxa exhibit metapopulation dynamics at regional scales (Borregaard and Rahbek 2010). In our study, the variables representing the carrying capacity for a species had no effect on the abundance of a species, while the propensity for dispersal was not related to distribution or abundance. This indicates that phytophagous true bugs might not be constrained by their dispersal ability. However, it is important to note that we did not directly measure the dispersal ability, but instead used morphological traits as proxies. A meta-analysis has shown, that the wingspan of butterflies is highly correlated to the dispersal ability, but its explanatory power was low (Sekar 2012). Nevertheless, a recent experimental study of red flour beetles (*Tribolium castaneum*) showed that dispersal is more strongly linked to morphological traits, namely leg length, than to physiological traits (e.g., metabolic rate; Arnold et al. 2017).

The habitat–dispersal hypothesis (Fig. 3.1.1f) suggests that even a weak disperser can attain high densities and a wide distribution independent of the propensity for dispersal, when dispersal success is determined by the amount

of available habitat in the landscape (Venier and Fahrig 1996, 1998, Fahrig 2013). Thus, high habitat-availability should increase dispersal success and therefore increase the distribution of the species. The hypothesis is often compared to or treated as similar to the resource-availability hypothesis. However, despite the causal link between habitat density and the distribution, rather than the abundance of a species, Venier and Fahrig (1996) clearly link habitat availability to dynamic processes. Thus, the hypothesis does not expect habitat availability to solely account for the distribution–abundance relationship, but rather to explain the deviations from the relationship that itself is shaped by population dynamics (i.e., an independent effect of habitat availability on distribution). Such positive independent effects of habitat availability have been found for several taxa, including stream insects (Heino 2005, Tonkin et al. 2016), amphibians (Rannap et al. 2009), diatoms (Heino and Soininen 2006), birds (Gregory and Gaston 2000) and fish (Tales et al. 2004). Next to a positive independent effect of habitat availability on distribution, we additionally proposed that this effect should be stronger for habitats of higher quality, since increasing habitat quality should further facilitate dispersal success. In our study, the amount of available habitat was determined by the density of the potential host plants of a species, with primary and secondary host plants representing high-quality and low-quality habitats, respectively. While secondary host-plants might be utilized for feeding, primary host-plants are also more often used for oviposition in many phytophagous true bugs and thus represent the available habitat in a landscape more accurately. The predicted causal structure of the habitat–dispersal hypothesis is strongly supported. The density of host plants had an independent positive effect on the distribution of species, while the causal link between distribution and abundance remained. This independent effect was stronger for the primary host-plants. The effect of primary host-plant density even surpassed the effect of mean abundance on the distribution of a species. These results appear to be robust and persisted after the exclusion of polyphagous species. For herbivores, an increasing dispersal success on sites with higher densities of host plants is an expectation of the resource concentration hypothesis, which states that herbivores are most likely to find and remain in patches with high densities of its host plants (Root 1973, Ralph 1977).

Conclusion

Understanding the processes leading to a positive distribution–abundance relationship of species has far-reaching implications for conservation efforts, as Lawton (1996) points out: (1) species could face a 'double jeopardy' when species with small range sizes also occur at low local densities, thereby increasing their vulnerability to human impacts; (2) a dynamic relationship between distribution and abundance might result in species not inhabiting all suitable habitats within its range when it occurs at low densities locally, and (3) human impacts that reduce the number of habitat sites regionally (e.g., habitat degradation or destruction) can reduce species densities even in remaining undisturbed sites, such as protected areas. Our study indicates that in order to maintain high abundances and broad distributions, herbivorous insects depend on high regional habitat availability. Thus, if the amount of suitable habitat decreases at the landscape scale, it might not be sufficient to protect single sites where species are locally abundant in order to prevent populations from going locally extinct. For the long-term facilitation of population dynamics, conservation efforts should aim at establishing

sufficient high-quality sites with high densities of potential habitat. This would maintain high abundances of focal species and would reduce their extinction probabilities in a landscape. Efforts to increase habitat availability, however, require detailed knowledge of habitat requirements of a species, which should be a reminder for ecologists not to neglect autecological studies.

Acknowledgments

We want to express our appreciation for the helpful comments of the handling editor and two anonymous reviewers that largely improved the manuscript. We thank the managers of the *Biodiversity Exploratories* and everyone involved. For extended acknowledgments see chapter 8.1. This work has been (partly) funded by the DFG Priority Program 1374 "Infrastructure-Biodiversity-Exploratories" (DFG-BR 1967/9-1, DFG-WE 3081/21-1). Field work permits were issued by the responsible state environmental offices of Baden-Württemberg, Thüringen, and Brandenburg (according to § 72 BbgNatSchG). We thank Ms. Karen Brune for proof reading the manuscript as a native English speaker.

Chapter 3.2

Mobility costs and energy uptake modulate the occurrence of butterflies

with

Stefan Pinkert | Dirk Zeuss | Martin M. Gossner | Roland Brandl | Stefan Brunzel

a modified version of this article is currently under consideration at *Nature Communitcations*

This paper is predominantly the contribution of the lead author Stefan Pinkert. My main contribution was the further development of the conceptual framework by the inclusion of species' habitat availabilities and emphasizing the causality between species' distributions and abundances. Here, I designed the methodology, compiled and analyzed data and substantially contributed to the writing and the revisions of the manuscript in close cooperation with the lead author. For me this manuscript is a follow-up on the previous article on the distribution-abundance relationship of true bugs. Therefore, we adopted the methodology, as well as the general causal framework surrounding distribution, abundance and habitat availability from the previous article. For this chapter, there is a digital supplement with additional data on the enclosed compact disk.

Summary

Current attempts to understand how morphological traits of species affect their distribution and abundance typically ignore the central assumption of trait-based approaches that these effects are mediated by the energy budget. Here, we use a causal ecophysiological framework centered on mobility costs and energy uptake of butterfly species to show that the effects of morphological traits can be offset by alternative energy uptake and allocation strategies. In particular, larger and darker species have wider distributions and are more abundant if they compensate for the energetic costs associated with an increase in size and melanisation by reducing mobility costs, increasing energy uptake, or both. Our findings highlight the potential of components of the energy budget not only as first-order predictors of variation in species distribution and abundance but also for elucidating the underlying physiological mechanisms and ultimately for understanding the functional significance of morphological traits.

Introduction

Within the last decades, morphological traits have increasingly been used to predict variation in the distribution and abundance of species in order to understand ecological processes (Brown et al. 2004, Violle et al. 2007, White et al. 2007, Angert et al. 2011) and species responses to climate change (Angert et al. 2011, Zeuss et al. 2014, Estrada et al. 2016, MacLean and Beissinger 2017). The presumed role of morphological traits for explaining this variation stems from the idea that these traits determine physiological performance and fitness of individuals and ultimately the vital rates of populations (Brown et al. 2004, Violle et al. 2007, Angert et al. 2011). Classic examples for relationships between morphological traits and physiology that can influence species distribution and abundance include effects of body size on development rate, metabolic rate, fecundity and dispersal ability (Damuth 1981, Honěk 1993, Gillooly et al. 2001, 2002, Brown et al. 2004, White et al. 2007). However, morphological traits generally leave a considerable part of variation in the distribution and abundance of species unexplained and the causes of this unexplained variation remain poorly understood (Blackburn et al. 1993, 2006, White et al. 2007, MacLean and Beissinger 2017).

Ectothermic organisms depend on thermal energy from their abiotic environment for activity and for maintaining fundamental physiological processes (Heinrich 1993, Gillooly et al. 2001, 2002). Ectotherms therefore evolved adaptations to the temperature regimes in which they live (May 1979, Zeuss et al. 2014, Pinkert et al. 2017). Two of the most important morphological traits that influence the physiology of ectotherms are their body size and color lightness (True 2003, Clusella Trullas et al. 2007, Angilletta et al. 2010). Larger species retain body heat more efficiently than smaller species owing to their lower surface-area-to-volume ratio, and darker colored species heat up faster than lighter colored species because they absorb more solar radiation (Kalmus 1941, Bogert 1949). Other benefits include enhanced immunocompetence of larger species (Vainio et al. 2004) and enhanced UV protection and pathogen resistance of darker species (Roulin 2014). Because of these functions, individuals of larger and darker ectothermic species often have a higher fitness than smaller and lighter-colored individuals (Honěk 1993, True 2003, Roff and Fairbairn 2013). However, increases in body size and melanisation are energetically costly (Gillooly et al. 2001, Talloen et al. 2004), which might have subsequent negative effects on the fitness of individuals (Roff and Fairbairn 2013).

Here, we argue that current attempts to understand how the distribution and abundance of species is affected by morphological traits such as body size and color lightness often fail to recognize alternative energy uptake and allocation strategies of species, as they consider these effects to be direct. Species might, for instance, compensate for the costs of beneficial morphological traits by allocating less energy to maintenance, growth and mobility or by increasing energy uptake. Only if the energy uptake exceeds the costs of an organism, energy can be allocated to dispersal and reproduction (Boggs and Freeman 2005, Boggs 2009).

The main fraction of the lifetime energy expenditure of ectotherms is used for mobility (Full 1997, Nagy et al. 1999, Niven and Scharlemann 2005), which increases with body size (Corben 1983). However, the energetic costs of mobility can be considerably reduced by enhancing the efficiency of locomotion through morphological adaptations. Such adaptations are especially relevant for flying species as the energetic costs of mobility are proportional to running speed but increase exponentially with wingbeat frequency (Full 1997, Niven and Scharlemann 2005). Thus, flying ectotherms would be able to allocate more energy towards dispersal and reproduction if they, for instance, reduce the energetic demand for each wingbeat and hence the costs of mobility through lower ratios of body-mass to wing-area (i.e. lower wing loads; Betts and Wootton 1988).

Alternatively, instead of reducing mobility costs, species could increase their energy uptake to compensate for the costs of maintenance, growth and mobility (Boggs and Freeman 2005, Boggs 2009) (Allocation Framework Theory). Theoretical and experimental evidence suggests that energy uptake and allocation strategies are related to a broad spectrum of morphological, ecological and life-history traits (Tiple et al. 2009, Arrese and Soulages 2010, Ohgushi et al. 2012, Stevens et al. 2012, Pélisson et al. 2013). For instance, species that do not forage as adults (i.e. capital breeders) are often smaller, live shorter and produce less offspring than those that take up energy (i.e. income breeders), because they need to pay for dispersal and reproduction from their energy reserves (Tammaru and Haukioja 1996, Stephens et al. 2009, Ohgushi et al. 2012). A variety of energy uptake and allocation strategies of species lies between these two extremes, spanning the so-called capital–income breeder continuum (Tammaru and Haukioja 1996, Stephens et al. 2009). However, in the absence of easily measured proxies for components of the energy budget, uptake and allocation strategies have been studied for only a few species and mostly under laboratory conditions (Hill 1989, Buckley 2008, Ohgushi et al. 2012, Pélisson et al. 2013, Llandres et al. 2015), and the importance of these strategies for the distribution and abundance of species remains unexplored (Stephens et al. 2009).

Here, we construct a causal framework according to the central assumption of trait-based approaches to integrate the effects of morphological traits on the energy budget and their ultimate influence on the distribution and abundance of species (Supplementary Fig. 1). Specifically, we test whether an increase in body size and a decrease in color lightness is associated with a reduction in mobility costs or an increase in energy uptake or both. Species that successfully compensate for their energetic costs via mobility costs and energy uptake should have wider distributions or higher abundances. To exemplify the importance of energy uptake and allocation strategies for the distribution and abundance of ectothermic species, we

use butterflies as model taxon. Butterflies are popular among enthusiast and professional entomologists, which has resulted in a unique pool of ecological knowledge and long-term monitoring data on this group, especially for the European continent. We consider only data on adult butterflies, because the allocation of energy completely shifts from growth and storage as larvae towards dispersal and reproduction as adult (Boggs and Freeman 2005). To assess energy uptake and allocation strategies of butterfly species associated with the main components of their energy budget, we propose two easily measured proxies: the wingbeat frequency as a proxy for mobility costs, assuming that species with a lower wingbeat frequency have a higher flying-efficiency and hence lower mobility costs, and the propensity for nectar foraging based on *in situ* images of adult butterflies as a proxy for energy uptake.

We found that mobility costs and energy uptake are important predictors of the distribution and abundance of species. Moreover, we show that these components of the energy budget mediate contrasting effects of body size and color lightness that ultimately influence the distribution and abundance of species. In particular, species that compensate for the costs associated with an increase in size and melanisation by reducing mobility costs or increasing energy uptake, have wider distributions and higher abundances. However, we also demonstrate that if alternative energy uptake and allocation strategies of species are not taken into account, the effects of morphological traits on the distribution and abundance of species can completely offset each other. These results stress the importance of integrating components of the energy budget of species into trait-based models for understanding the mechanisms that link morphological traits, physiological performance and the occurrence of species and ultimately for improving predictions of species distribution and abundance.

Methods

Proxies for mobility costs and energy uptake.

As a proxy of the energetic costs of mobility, we measured the wingbeat frequency of 316 individuals of 102 butterfly species using high-speed camera footage taken during the years 2013 to 2017 at different sites in Central Europe (a total of 793,896 frames or 2,646 s; for details see chapter 8.2 and for an example film clip see Digital Supplementary). The wingbeat frequency of a species in Hz was calculated as wingbeat counts of each scene divided by its length (in s). Subsequently, wing beat frequencies were averaged across individuals (median: 3 individuals, min: 1 individual, max: 9 individuals). To integrate across the peak and normal mobility costs of a species, we averaged wingbeat frequencies during *in situ* and escape flight (Fig. 3.2.1c). When only normal or peak wingbeat frequencies were available for a species (1 and 43 species, respectively), we used values that were predicted based on the relationship between these two variables (Fig. 8.2.2). Furthermore, while filming, we also recorded the ambient temperature to evaluate whether the wingbeat frequency of species was temperature dependent. However, the correlation between these two variables was not significant (Supplementary Fig. 8.2.3).

Adult butterflies are mainly generalist nectarivores (Ebert and Rennwald 1993a), and experimental evidence suggests that the sugar concentrations of flowers visited by butterflies are similar because of ecological and physical constraints (Krenn 2010, Kim et al. 2011) (for details see chapter 8.2). We therefore assumed

that species that spend more time collecting nectar during a given timespan take up more energy than species that spend less time collecting nectar. Following an approach that has been successfully applied to extract data on the geographical variation in phenotypic traits (Leighton et al. 2016), we counted how often individuals were observed collecting nectar on flowers based on the results of a Google Images search (accessed on May 15, 2017). To avoid potential bias of the access point, which could result from Google's search algorithms, we used the international homepage (i.e. google.com) and searched for the scientific name of a butterfly species. Of the first 100 hits, only images of clearly identifiable and living adult individuals were used for further analyses. We assigned each image a value of 1 or 0 depending on whether the individual was observed foraging or not, and a value of 0.5 if it sat on a flower but the proboscis was not visible and finally averaged these values for each species (Fig. 3.2.1e). A rarefaction analysis showed that standard deviations calculated for increasing numbers of randomly sampled images of species remains constant at 0.04 for sample sizes above 32 images (Fig. 3.2.1e). This suggests that our results are not affected by differences among locations and conditions of these observations and, although we used all images sampled for further analyses, it indicates that relatively small numbers of images are already sufficient to provide a robust estimate for the propensity of nectar foraging of a species. The reliability of our approach was further confirmed by a positive relationship between image-based estimates and expert classifications of the nectar foraging propensity of species ($p < 0.001$, rho = 0.31, n = 436; for details and the comparison, see Fig. 8.2.4).

Morphological traits

Estimates of the color lightness, body size and wing load of a species were calculated based on scanned dorsal drawings of European butterfly species taken from Tolman and Lewington (2008). Based on images of the body surfaces of species, we calculated the average RGB of pixels as an estimate of the color lightness, ranging from 0 (absolute black) to 255 (pure white) and the sum of volumes of each pixel row [$\pi \times (\frac{1}{2}$ length of pixel row$)^2 \times$ pixel edge length in cm] as an estimate of the body volume of a species using functions of the R package *png* (Urbanek 2013; data taken from Zeuss et al. 2014, 2017). We decided to use body volume instead of body length or area because this three-dimensional measure represents a better approximation of the body mass of a species. The wing load of a species was calculated by dividing its body volume by the wing area (the number of pixels of all wings $\times$ pixel area in cm^2; Betts and Wootton 1988).

Distribution and abundance of species

Regional distributions were estimated based on gridded distribution data of species across Europe [in a grid of cells with a size of 50 km $\times$ 50 km, CGRS; data taken from Zeuss et al. (2014); original distribution maps are from Kudrna et al. (2011). Data for Belarus, the Ukraine, Moldova and Turkey were excluded because according to the authors, distributional data for these countries are incomplete and in part unreliable. In addition, we excluded all cells with less than 50% land cover and all islands except Great Britain and Ireland. For each species, regional distributions were calculated by dividing the number of grid cells in which it was present by the total number of grid cells (1,825 grid cells, i.e. regional occupancy).

To calculate the local abundance and distribution of species, we used survey data for

butterfly species assessed as part of the Biodiversity Monitoring Switzerland during the years 2003–2016 (www.biodiversitymonitoring.ch, accessed on October 4, 2017). The monitoring scheme involved the collection of butterflies along 520 regularly placed sites (in a grid of cells with a size of 5 km × 5 km) at which species were sampled on transects of 2.5 km length. Transects were visited four to seven times each year during comparable weather conditions. Species abundances were calculated as the average number of individuals per occupied transect and year (i.e. population density). Note that this abundance measure is not correlated with the number of generations per year (Fig. 8.2.5). Although regional and local distributions of species should be strongly related (Brändle and Brandl 2001b), we also considered local distributions of species (i.e. proportion of occupied transects) in our analysis to account for differences in the spectrum of regionally and locally available habitats that can result in negative distribution–abundance relationships (Gaston and Lawton 1990).

Habitat availability

We were particularly interested in the importance of functional traits of species (i.e. intrinsic drivers) of their distribution and abundance. However, previous studies have shown that the distribution and abundance of phytophagous insects is also influenced by the availability of their habitat (Curtis et al. 2015, Friess et al. 2017). To account for the effect of host plant availability on the distribution and abundance of species, we used gridded distribution information on all 473 larval host plants of butterflies in Switzerland for the years 2003–2016 from the Info Flora Database (accessed on October 18, 2017; a grid of cells with a size of 5 km × 5 km). Information on larval host plants was compiled from Bräu et al. (2013) and Ebert and Rennwald (1993a, 1993b). Based on these data, we then calculated the habitat availability for each butterfly species as the number of grid cells occupied by host plants divided by the total number of grid cells across Switzerland.

Statistical analyses

The distributions of all variables were reviewed and transformed if necessary (for model residuals and histograms of variables see Figs. 8.2.6 and 8.27). To normalize the data, nectar-foraging propensity, habitat availability, local range size and regional range size were logit transformed, and wingbeat frequencies, body volume, color lightness, wing load and local abundance were $\log_e$ transformed. We tested whether mobility costs and energy uptake mediate the effects of morphological traits on the distribution and abundance of species using confirmatory path analyses (Shipley 2004) as implemented in the R package *piecewiseSEM* (Lefcheck 2015). This approach allows us to fit a set of linear mixed-effects models in a single causal framework to test hypotheses about relationships of interacting variables and for evaluating the direct and indirect effects of predictor variables on the responses. Here, we fitted two main model sets as the basis for the confirmatory path analyses (Fig. 3.22 and Table 8.2.1). In the first path analysis, we tested for direct effects of morphological traits (body volume, color lightness and wing load) on the distribution and abundance of species (regional distribution as well as local distribution and abundance). In the second path analysis, we tested for direct effects of morphological traits on mobility costs and energy uptake, and for direct effects of mobility costs and energy uptake on the distribution and abundance of species. Both path analyses included a direct effect of habitat availability on the local distributions

of species and direct effects of local abundance on local distribution and vice versa. By assessing the phylogenetic signal of species traits based on the most recent phylogeny of all European butterflies (Zeuss et al. 2014; R package *phytools;* Revell 2017), we showed that wingbeat frequencies, nectar-foraging propensities of species and all morphological traits considered in the analysis carried a strong phylogenetic signal (Fig. 3.2.1d). To meet the general assumption of statistical tests that all data points are independent from each other, we therefore fitted component models with a nested random intercept to account for the phylogenetic relationship of species (genus nested in subfamily and subfamily nested in family) using the *lme* function in the R package *nlme* (Pinheiro et al. 2017). Note that the phylogeny of European butterflies is in accordance with the taxonomic classification used in piecewise structural equation models (Tolman and Lewington 2008). Models including a random effect of the phylogenetic relationship of species consistently explained a higher proportion of variance than models without (i.e. conditional R^2 > marginal R^2; Table 3.2.1) indicating that the intercepts of the analyzed relationships differed between clades.

Although most of the predicted relationships were significant for the model including mobility costs and energy uptake, Fisher's *C* statistics indicated that some relevant paths were missing. Following Shipley (2004), we therefore added the most important and significant predictor variables (highest effect size) one at a time to the models and repeated the evaluation of the conditional independence claims until this criterion was met (Table 8.2.1). Based this model evaluation, two missing paths were added to the models: an effect of regional distribution on local abundance and an effect of wingbeat frequency on regional distribution. In a second step, least important and insignificant paths were removed one at a time. Multicollinearity among predictor variables was evaluated by calculating the variance inflation factor from variance–covariance matrices of mixed-effects models (Zuur et al. 2009). For all our models, variance inflation factors smaller than 2 indicated minor collinearity among predictor variables (Table 8.2.1).

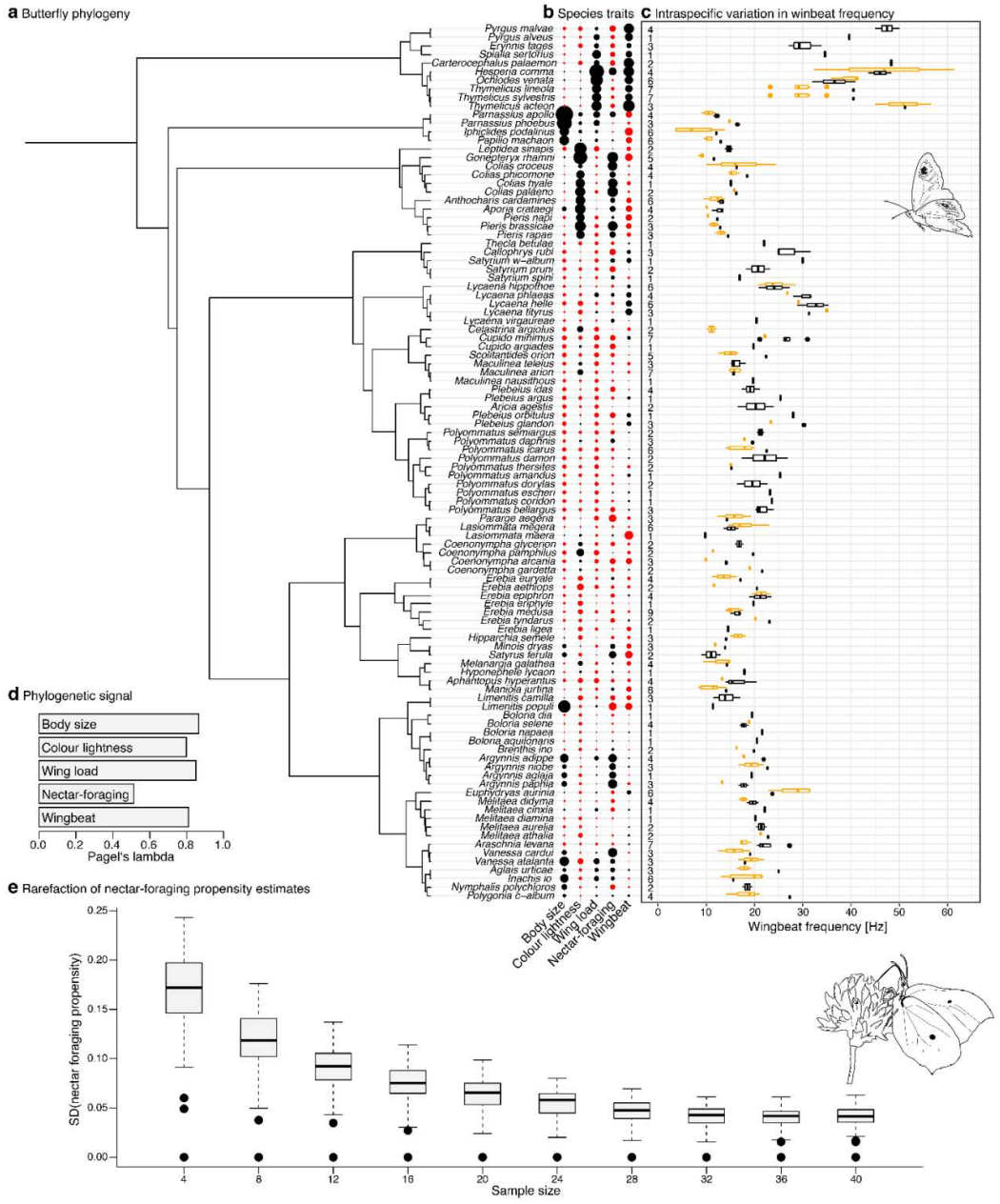

FIGURE 3.2.1. Summary of the data on 102 European butterfly species that have been used in the present study. **a** The phylogeny, **b** morphological traits and proxies for the mobility costs and energy uptake of butterflies, **c** the intraspecific variation in normal (black) and peak (orange) wingbeat frequencies, and **d** the phylogenetic signal in the presented traits of 102 European butterfly species. **e** Standard deviation of nectar-foraging propensities of butterfly species calculated for randomly sampled images using different sample sizes. Dots sizes in **b** indicate negative (red) and positive (black) standard deviations from the mean of each trait, ranging from approximately -3 to 4. In **c** values on the left indicate the number of individuals per species filmed. Traits in **b** and **c** are ordered according to the phylogeny. Bars in **d** indicate the strength (Pagels's lambda) of phylogenetic signals of traits calculated based on branch length from the phylogeny of all European butterfly species (Zeuss et al. 2014). All phylogenetic signals were significant at $p < 0.001$. Copyrights for the icons of *Lasiommata meara* in c and *Gonepteryx rhamni* in e are held by SP.

TABLE 3.2.1. Summary of piecewise structural equation models.

Response	Abundance$_{CH}$	Distribution$_{CH}$	Distribution$_{EU}$	Habitat availibility$_{CH}$	Body size	Color lightness	Wing load	Wingbeat	Nectar-foraging	R^2_M	R^2_C
Model 1											
Abundance$_{CH}$		+6.24***	–3.84***							0.23	0.52
Distribution$_{CH}$	+4.16***			+4.39***						0.29	0.63
Distribution$_{EU}$		+6.23***		+2.45*						0.42	0.58
Model 2											
Abundance$_{CH}$		+6.04***	–4.03***		–2.57**				+2.27*	0.29	0.54
Distribution$_{CH}$	+3.49**			+4.73***					+2.08*	0.34	0.61
Distribution$_{EU}$		+7.86***						–2.09*		0.42	0.59
Nectar-foraging					+2.83**	+2.45*				0.20	0.64
Wingbeat					–9.03***	– 2.37**	+8.80***			0.66	0.79

Notes. Standardized effect sizes (z-scores) of predictors and explained variance (marginal/conditional R^2, i.e. without/with a random effect of genus nested in subfamily and subfamily nested in family) from models that test for direct effects of morphological traits on the distribution and abundance of 102 European butterfly species (Model 1) and indirect effects via proxies for mobility costs and energy uptake (Model 2). Models correspond to the path diagrams in Figure 3.2.2. The subscripts CH and EU refer to variables calculated for Switzerland and Europe, respectively. *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$.

Results

Alternative energy uptake and allocation strategies

As proxies for energy uptake and allocation strategies of butterfly species associated with the two main components of their energy budget, we first assessed wingbeat frequencies of 102 butterfly species based on high-speed camera footage and their nectar-foraging propensities by estimating the relative time species spent collecting nectar (Fig. 3.2.1). We combined these data with information on species distributions across Europe and long-term monitoring data from Switzerland and with estimates of the body size, color lightness and wing load of species from standardized images (see *Methods*). We tested whether morphological traits affect the distribution and abundance of species directly or indirectly via mobility costs and energy uptake using piecewise structural equation models. To account for the potential confounding effect of wing size on the wingbeat frequency, we included the wing load of butterfly species (i.e. the ratio of body volume to wing area) into the models. In addition, we considered habitat availability (i.e. occupancy of larval host plants) as a potential constraint on the maximum distribution of species. Furthermore, the models contained a nested random factor to account for the phylogenetic relatedness (Fig. 3.2.1a-d; see *Methods*).

In models that tested for direct effects, we found that none of the considered morphological traits had a significant effect on the distribution and abundance of species (Fig. 3.2.2, Model 1). In models that accounted for energy uptake and allocations strategies of species, however, morphological traits significantly affected the distribution and abundance of species via wingbeat frequency and nectar-foraging propensity (Fig. 3.2.2, Model 2). In both models, local habitat availability positively affected local distribution, local distribution positively affected regional distribution, and regional distribution negatively affected local abundance (Fig. 3.2.2; Table 3.2.1). Local distribution and abundance positively affected each other.

Predictors of the distribution and abundance of species

We assessed the importance of effects of morphological traits on proxies for components of the energy budget and ultimately on the distribution and abundance based on path coefficients and total effect sizes of predictor variables in the overall models. The former indicates the strength of a single direct effect, whereas the latter indicates the sum of all direct and indirect effects (i.e. the product of multiple direct effects) of the predictor on the response variables. Body size and color lightness negatively affected the wingbeat frequency of species and positively affected the nectar-foraging propensity of species (Fig. 3.2.2). In addition to its indirect positive effects on the distribution and abundance of species, body size also had a direct negative effect on local abundance. Total effect size indicated that wingbeat frequency and nectar-foraging propensity were consistently important predictors of the distribution and abundance of species (Fig. 3.2.3). Species with higher wingbeat frequencies had smaller regional distributions than species with lower wingbeat frequencies, and species with a higher nectar-foraging propensity had both higher local abundance and wider local distributions than species with a lower nectar-foraging propensity. The hypothesized effects of wingbeat frequency on both local abundance and local distribution were not significant.

Discussion

Our study aimed at integrating morphological traits and components of the energy budget into trait-based models for understanding how energy uptake and allocations strategies of species influence the occurrences of species. Using a causal ecophysiological framework centered on mobility costs and energy uptake of species, we demonstrate that alternative energy uptake and allocation strategies of butterfly species mediate the effects of morphological traits on distribution and abundance. Larger and darker-colored species have wider distributions and are more abundant than smaller and lighter colored species if they compensate for the costs associated with an increase in size and an increase in melanisation by reducing mobility costs or increasing energy uptake. By accounting for energy uptake and allocation strategies, we exemplify that body size and color lightness have contrasting effects on the distribution and abundance of species that are otherwise obscured.

In line with several previous studies that reported weak and insignificant size-abundance relationships for other ectothermic taxa (Blackburn et al. 1993, 2006, Friess et al. 2017), we demonstrated that body size does not directly affect the abundance of butterfly species. By contrast, accounting for species' energy uptake and allocation strategies allowed establishing several indirect effects of body size on species' distribution and abundance and a negative effect of body size on the abundance of species that reflects the increase in maintenance costs associate with an increase in body size (Brown et al. 2004, White et al. 2007). This exemplifies that, especially in ectotherms which have relatively low maintenance costs (Nagy et al. 1999), alternative energy uptake and allocation strategies contribute to the scatter in size-abundance relationships because species compensate these costs by reducing mobility costs or increasing energy uptake.

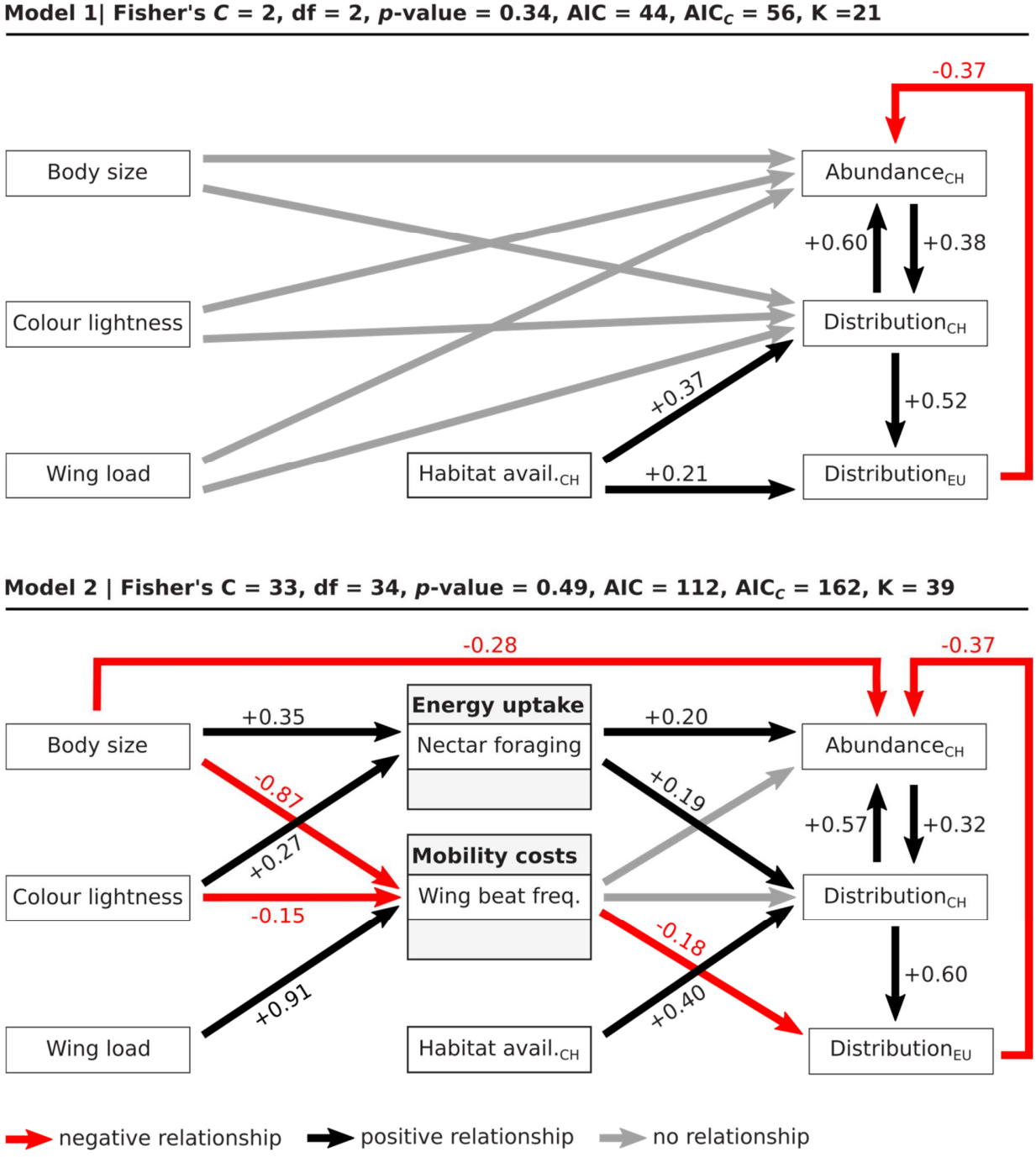

FIGURE 3.2.2. Mobility costs and energy uptake mediate contrasting effects of morphological traits on the distribution and abundance of species. Results from piecewise structural equation models that test for direct effects of morphological traits on the distribution and abundance of 102 European butterfly species (Model 1) and indirect effects via proxies for mobility costs and energy uptake (Model 2). Values above each arrow indicate scaled regression coefficients of significant paths ($P < 0.05$). Insignificant paths (grey arrows) were excluded from the final model. Significant *P*-values of the Chi-squared significance test ($p > 0.05$) and associated statistics from directed separation tests (Fisher's C and degrees of freedom) above each diagram indicate that the models contain all significant paths. Additional statistics include scores for Akaike Information Criterion (AIC), corrected AIC (AIC_C) and likelihood degrees of freedom (K). The subscripts CH and EU refer to variables calculated for Switzerland and Europe, respectively.

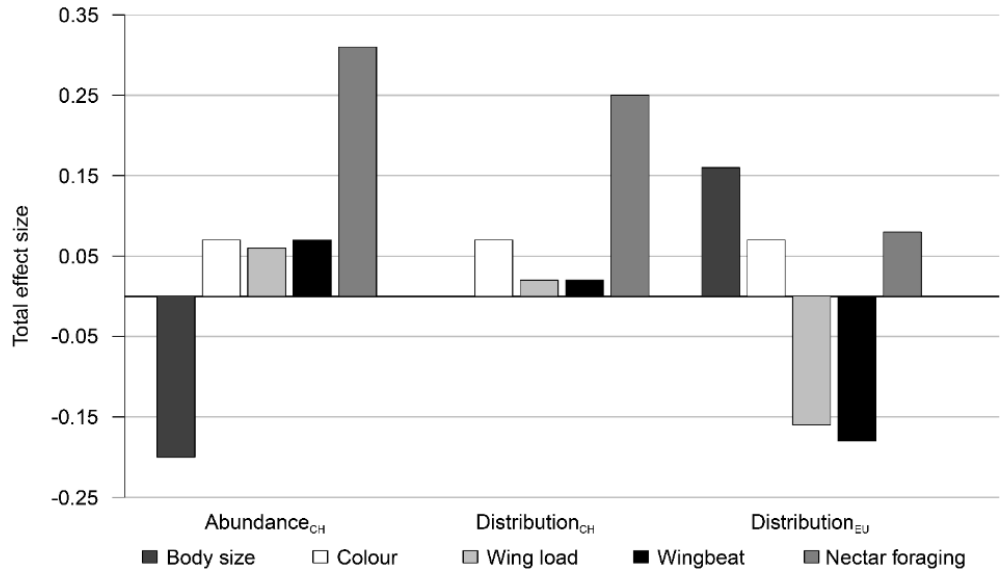

FIGURE 3.2.3. Mobility costs and energy uptake are important predictors of distribution and abundance of species. Bars indicate total effect sizes of morphological traits and proxies for mobility costs (wingbeat frequency) and energy uptake (nectar-foraging propensity) on the distribution and abundance of 102 European butterfly species. Total effect sizes represent the sum of all significant direct and indirect effects (products of coefficients along indirect paths) of each predictor on the response variable in piecewise structural equations (see Model 2, Fig. 3.2.2). The subscripts CH and EU refer to variables calculated for Switzerland and Europe, respectively.

Following the considerations for body size, darker colored species should have wider distributions and higher abundances if they successfully compensate the energetic costs of melanisation via mobility costs and energy uptake.

Our results generally support this prediction, but the uptake and allocations strategies associated with color lightness were the opposite of what we expected. We showed that darker colored species had higher wingbeat frequencies and spent less time collecting nectar than lighter colored species, which negatively affected their distribution and abundance. These results demonstrate that color-based heat gain enables darker species to have relatively high wingbeat frequencies despite low concurrent energy uptake, suggesting that although melanin is energetically costly (Talloen et al. 2004) an investment into melanin might be inevitable for the activity and development of some ectothermic species, for instance, under extremely low temperatures as well as high humidity and UV radiation (Clusella Trullas et al. 2007, Zeuss et al. 2014, Pinkert et al. 2017, Heidrich et al. 2018). Furthermore, our results suggest that, instead of decreasing mobility costs or increasing energy uptake, the costs of melanization might be compensated by other components of the energy budget, including larval energy uptake and development (Talloen et al. 2004).

Nevertheless, whether color lightness influences species' life-histories is still an ongoing debate (True 2003, Heidrich et al. 2018, Pinkert and Zeuss 2018).

Insects rely on body fat allocated from concurrent energy uptake as adults and larval fat reserves to account for dispersal and reproduction (Boggs 2009). Therefore, mobility costs, which constitute the main fraction of the lifetime energy expenditure of

ectothermic taxa (Nagy et al. 1999), and propensity for foraging should provide important constraints to the distribution and abundance of insects. Consistent with the conclusions of previous theoretical and experimental studies (Hill 1989, Boggs 2009), our results suggest that butterfly species with lower wingbeat frequencies or higher nectar-foraging propensity can allocate more energy to body fat reserves because of their reduced mobility costs and increased energy uptake. Moreover, we demonstrate that the effects of components of the energy budget on dispersal and reproduction influence the occurrence of species both directly and indirectly via the dynamic distribution-abundance relationship (Fig. 3.2.2).

Despite differences in occurrence between species with high and low mobility costs or energy uptake, it is important to note that these strategies should be equally successful. Community-wide analyses indicated that the foraging propensity of species is linked to their life-history and phenology including, for instance, the timing (Tammaru and Haukioja 1996, Ohgushi et al. 2012, Pélisson et al. 2013) and length of periods of activity (Tammaru and Haukioja 1996, Stephens et al. 2009). We showed that the distribution and abundance of butterfly species is constrained by the availability of their habitat but modulated by alternative energy allocation and energy uptake strategies of species (Fig. 3.2.2).

Together with the finding that, mobility costs and nectar-foraging propensity differed strongly between clades (Fig. 3.2.1a-d; Table 3.2.1), our results therefore suggest that the evolution of alternative energy allocation and energy uptake strategies contributes to the partitioning of locally available resources among species through time.

The increasing availability of data on functional traits, geographic distributions and abundances of species from monitoring campaigns together with research challenges in the face of rapid climate change have reinvigorated a mechanistic perspective on ecology (Brown et al. 2004, Crozier and Dwyer 2006, Kearney and Porter 2009, Buckley et al. 2010, Angert et al. 2011). Our results suggest that easily measured proxies for components of the energy budget, such as wingbeat frequencies of flying or the running speed of ground-dwelling species (Full 1997) as well as foraging propensities of species or the duration of plant-animal interactions (Memmott et al. 2007), can complement our tools for understanding the physiology and ecology of ectothermic organisms. We showed that mobility costs and energy uptake mediate contrasting effects of morphological traits on the species distribution and abundance. Importantly, we demonstrate that these contrasting effects can offset each other when they are assumed to be direct. Thus, ignoring energy uptake and allocation strategies of species can lead to an underestimation of the functional significance of morphological traits and to false conclusions about the mechanisms underlying variation in species' distribution and abundance. We are therefore convinced that integrating proxies for components of the energy budget into mechanistic models (Crozier and Dwyer 2006, Kearney and Porter 2009, Buckley et al. 2010, Llandres et al. 2015) will help to understand differences in life histories and population dynamics of species and that the herein presented insights will improve the accuracy of predictions of species' distributions and population trends based on functional traits.

Acknowledgments

We sincerely thank S. Fritz for comments on an earlier version of the manuscript. NF was supported as a doctoral student by the Rudolf and Helene Glaser Foundation organized in the "Stifterverband für die deutsche Wissenschaft". We also thank Helga and Dietrich Wagler, Hermann-Josef Falkenhahn, Armin Six and Ralf Bolz for classifying the propensity for nectar foraging of butterfly species based on their experience, and Dieter Schneider for species identification and counting nectar foraging individuals based on Google images. We acknowledge the Swiss Federal Office for the Environment (FOEN) and the National Data- and Information-Centre of the Swiss Flora (Info Flora) for the permission to use the data from their monitoring programmes.

Chapter 4.1

The dark side of Lepidoptera: Color lightness of geometrid moths decreases with increasing latitude

with
Lea Heidrich | Konrad Fiedler | Martin Brändle | Axel Hausmann | Roland Brandl | Dirk Zeuss |

published in Global Ecology and Biogeography, 27 (4), 2018, p. 407 – 416

This paper is predominantly the contribution of the lead author Lea Heidrich. I contributed strongly to the conceptual framework of the manuscript as well as the analysis and especially the interpretation of the data. Furthermore, I formulated large parts of the manuscript and strongly contributed to the revisions during peer-review. For this chapter, there is a digital supplement with additional data on the enclosed compact disk.

Summary

The observed decrease in insect color lightness with increasing latitude has been explained in earlier macroecological studies by the increased solar absorption of dark coloration, which allows extended periods of activity. However, melanin-based dark coloration also protects against pathogens and UV radiation, which select for dark coloration at low latitudes where these selection pressures intensify. In nocturnal insects, the relative importance of these protective functions of dark coloration is expected to surpass thermoregulatory functions, as nocturnal species cannot benefit from extended periods of activity during the daytime. Hence, we expected that diurnal and nocturnal insects show contrasting geographical patterns of color lightness. We tested these predictions using geometrid moths, which comprise both diurnal and nocturnal species. We used digital image analysis to assess color lightness of 637 species, compiled their distribution across 3,777 grid cells of 50km × 50km and calculated the assemblage-based average color lightness. We used multiple regressions, autoregressive error models and randomizations to test for relationships between color lightness and environmental variables associated with the thermal environment, putative pathogen pressure, and UV radiation. We found a clear decrease in color lightness of assemblages of both diurnal and nocturnal moth species with increasing latitude. In every model, solar radiation was the most important predictor of color lightness, i.e. color lightness consistently increased with increasing solar radiation. These results indicate that the thermal environment is the most influential climatic driver of insect color lightness – independent of thermoregulatory strategy and nocturnal or diurnal activity. This challenges the view that extended periods of activity are the main selection pressure for geographical variation in insect color lightness. Consequently, the relationship between insect color lightness and the thermal environment might be more general than previously thought.

Introduction

Large-scale variation in environmental conditions shape species assemblages by selecting for traits that enhance physiological and ecological performance (Violle et al. 2014). The analysis of the variation of species traits along environmental gradients thus offers an opportunity for understanding the involved selection pressures.

The earliest example of a macroecological pattern in species traits is the variation in color lightness of animals, which describes the quantity of reflected light irrespective of its wavelength and is mainly regulated by melanin pigments. (Gloger 1833) observed that endothermic vertebrates are typically more darkly colored near the equator than near the poles. Presumably, melanin-based dark coloration protects against pathogen pressure and UV radiation, which are highest at low latitudes (Mackintosh 2001, Burtt and Ichida 2004, Caro 2005). Recent studies revealed contrasting geographical patterns in the color lightness of insects, the majority of which are ectothermic. Among insects, darker-colored species occur at high latitudes presumably because of the thermoregulatory advantages of dark coloration (Zeuss et al. 2014, Schweiger and Beierkuhnlein 2015, Bishop et al. 2016, Pinkert et al. 2017). Hence, whether dark or light coloration is favored in a particular environment might depend on different selection pressures that operate simultaneously and are not mutually exclusive but vary in their relative importance depending on the physiology and behavior of animals.

All macroecological studies of insects published so far have interpreted the observed pattern of a decrease in color lightness with latitude in the context of the thermal melanism hypothesis (Clusella Trullas et al. 2007, Zeuss et al. 2014, Bishop et al. 2016, Pinkert et al. 2017). According to this hypothesis, dark coloration increases absorption of solar radiation and hence allows dark-colored insects to heat up faster and attain higher steady-state body temperatures compared to light-colored insects (Gates 2003). These differences could result in extended periods of activity, which in turn might increase, e.g. mating success or feeding rates (Gates 2003, Clusella Trullas et al. 2007). Thus, dark coloration of insects should be advantageous in cold environments, whereas light coloration is expected to be favored in warm environments to prevent overheating (Clusella Trullas et al. 2007, Zeuss et al. 2014). However, Bishop et al. (2016) observed that the color lightness of ant assemblages along elevational gradients increases with temperature but also decreases with UV radiation. These findings suggest that the relative importance of thermal melanism might decrease in relation to other functions of melanin pigments, depending on environmental conditions and the corresponding selection pressures. Melanin pigments deposited in the epidermis or cuticle protect against cell damage and oxidative stress by absorbing harmful UV radiation (Majerus 1998). In addition to the protection against UV radiation, melanin embedded in animal tissues increases the resistance against viral, bacterial and fungal pathogens (Wilson et al. 2001, Mackintosh 2001, True 2003, Mikkola and Rantala 2010, Dubovskiy et al. 2013). Melanin neutralizes intrusive pathogens by encapsulation and reduces their infection rates by generally strengthening the cuticle (Wilson et al. 2001, True 2003, Mikkola and Rantala 2010, Dubovskiy et al. 2013).

Each of these functions of melanin-based coloration viewed separately should lead to distinct geographical patterns in the average color lightness along environmental gradients. If only the thermoregulatory function of melanin were of importance, we would observe a decrease in color lightness with latitude and elevation, following thermal gradients. Then again, if only protection against UV radiation were of importance, we would observe an increase in color lightness with latitude as UV radiation decreases towards the poles but also a decrease in color lightness with elevation as UV radiation increases with elevation. Finally, if the protection against pathogens were the sole driving force of the geographical variation in insect color lightness, we would observe a decrease in color lightness in warm (e.g. at low latitudes and elevations) and/or humid environments, where pathogen pressure and biotic interactions are assumed to be highest (Reilly et al. 2014, Yin et al. 2016).

Studies of diurnal insects in general support the view that the major driver of geographical patterns in color lightness is the thermal environment, as expected by the thermal melanism hypothesis. Although it seems obvious that thermoregulatory constraints favor a decrease in insect color lightness with increasing latitude, the relative importance of this function might change with different thermoregulatory strategies. Notably, the literature on insect coloration is strongly biased towards diurnal insects, for which thermal melanism is a likely explanation for the geographical variation in their color lightness. However, nocturnal insects have no thermoregulatory benefit from dark or light coloration for extending their period of activity. Thus, the relative importance of the above-

mentioned protective functions of melanin-based coloration is higher in nocturnal insects, which should lead to contrasting geographical patterns in the color lightness of nocturnal insects compared to diurnal insects along environmental gradients.

In this study, we focused on the geographical variation in color lightness of assemblages of geometrid moths. This species-rich family of lepidopterans comprises both nocturnal and diurnal species. Geometrid moths furthermore differ from taxa previously used in macroecological studies of insect color lightness in their thermoregulatory strategies. Due to their low body mass (~ 0.02–0.22 g, (Casey and Joos 1983), convective cooling compromises solar absorption and storage of the energy gained (Heinrich 1993). The strategy of geometrid moths is instead based on a small wing load, which allows an energetically inexpensive flight activity of many species even at low temperatures (Casey and Joos 1983, Heinrich 1993, Utrio 1995). However, thermoregulation through dark or light coloration might still be advantageous for diurnal geometrid moths. Furthermore, depending on the choice of resting spots during the day, which spans a wide range of shaded or non-shaded substrates (e.g. rocks, bark, or the upper side of leaves in the case of *Mesoleuca albicillata* and other species that mimic bird droppings), moths are exposed to either direct or diffuse UV radiation (Parisi et al. 2000). Considering that UV radiation increases oxidative stress in adults of several moth species (Zhang et al. 2011, Ali et al. 2016), dark-colored moths should be favored in areas with high UV radiation. Additionally, Mikkola and Rantala (2010) proposed that selection for pathogen resistance might be responsible for changes in the frequency of melanic forms of moths. Thus, if the probability of pathogenic infections is higher in warm (Yin et al. 2016) and/or humid (Reilly et al. 2014) environments, dark-colored moths should be favored there.

Here, we investigated the relative importance of the above-outlined functions of melanin-based coloration by analyzing the covariation of the average color lightness within assemblages of 637 species of geometrid moths across the Western Palearctic and environmental variables associated with the thermal environment, UV radiation and putative pathogen pressure. We expected that i) the color lightness of assemblages of nocturnal species decreases in humid and/or warm environments to protect against pathogens and ii) decreases with solar radiation to protect against UV radiation. These expectations rest on the assumption that the thermoregulatory benefit of dark or light coloration of extending the period of activity should not apply for nocturnal insects. As this benefit should apply for diurnal insects, we expected that iii) the color lightness of assemblages of diurnal species increases with increasing solar radiation, which should lead to contrasting geographical patterns of color lightness between nocturnal and diurnal species.

Methods

Species data

The analyzed species data are based on the monograph series "The Geometrid Moths of Europe Vols. I–IV" (see chapter 9 for data sources), which include the subfamilies Archiearinae, Orthostixinae, Desmobathrinae, Alsophilinae (in recent taxonomy transferred to Ennominae), Geometrinae, Sterrhinae and Larentiinae and covers approximately 65% of the total geometrid fauna of the Western Palearctic. All of the missing geometrid moth species belong to the subfamily Ennominae, which has

not yet been completely covered in the monograph series. Adults of some geometrid moths are also active during the day. To account for this behavioral trait, we separated 637 species with information on distribution and color lightness (hereafter referred to as the Geometridae data set) into strictly nocturnal geometrid moths (160 species) and diurnal geometrid moths (109 species). Classification as strictly nocturnal or diurnal geometrid moths was based on species accounts cited in Appendix 1 and our own field observations. The majority of species (368) could not be definitively classified because of a lack of reliable information. Although it is likely that these species are mainly nocturnal (for example, all are regularly attracted to light traps), they were not included in the strictly nocturnal data set. In addition, geometrid moths that fly at dusk or dawn or that can be startled during daylight were not assigned to either the nocturnal or diurnal subset, but are included within the complete data set. Note that the proportion of diurnal species increases towards the north (Tabl1 9.1.1). Furthermore, day length increases with increasing latitude during summer, and the temporal window for strict nocturnal activity decreases accordingly (chapter 9.1).

Distribution maps were available for 654 species. We digitized contour distribution maps of these species using the software WORLDMAP (Williams 2001), which allows the exploration of grid-based species richness. For each species, WORLDMAP grid cells with a resolution of 50 km × 50 km were marked as "species present" if covered by the species distribution map. Our study covered the Western Palearctic, ranging from the Mediterranean area and Black Sea in the south to the Ural Mountains in the east, the British Isles in the west and northernmost Fennoscandia in the north. Coastal grid cells (defined as <50% land mass) and grid cells with less than five recorded species were excluded from our analysis to improve the information quality of the data. This resulted in a total of 3,777 grid cells for the Geometridae data set, 3,614 grid cells for the nocturnal species data set and 3,775 grid cells for the diurnal species data set (Digital Supplementary). For a list of all included (637) and excluded (17) species with no distributional information, see Digital Supplementary.

Digital image analysis

Color lightness, i.e. whether a colored object appears to be lighter or darker colored than others under similar light conditions, is the most basic characteristic of coloration. It can be calculated using the arithmetic mean of the red, green and blue color (grey value), and is darkest (black) with zero intensity and lightest (white) with full intensity of reflected light. To assess the color lightness of the moth species, we scanned the photographs of museum voucher specimens published as color plates within "The Geometrid Moths of Europe" monograph, which includes 3,443 images of 680 species, with an EPSON Perfection 4490 Photo Scanner (2400 dpi, 24 bit, RGB color space). After printing a test copy of the color plates, the coloration was standardized such that the coloration of the printed color plates in the monograph series matched the original coloration of the specimens. After scanning the plates from the monograph series, we removed the background and converted the images to 8-bit grey values (Zeuss et al. (2014). Color lightness was scaled to range from 0 (completely black) to 1 (completely white) using the package png (Urbanek 2013), which processes raster images in the R environment. In the next step, color lightness values were averaged across all pixels of each image. If several images of one

species were available or if subspecies were depicted, they were also averaged to arrive at one representative value for each species (Table S2). We used the full dorsal surface area of the body and wings to calculate the color lightness of species. As there was no significant sexual dimorphism in color lightness (Appendix S2, Figure S2.2), we used all available images per species without considering sex. Only the few images of brachypterous females were excluded because short or reduced wings might be a special strategy of adaptation to cold environments (Wahlberg et al. 2010).

Environmental variables

Temperature and UV radiation are highly correlated (Appendix S3, Figure S3.3). We thus used solar radiation as a surrogate for both temperature and UV radiation to address the possible protective function of melanin as well as its potential thermoregulatory roles among diurnal moths. This is adequate because the thermoregulatory function should lead to a positive correlation between color lightness and radiation, whereas the protective function should lead to a negative correlation, which allows a separation of the two effects. The Microclim dataset (Kearney et al. 2014) provides estimates of clear sky solar radiation and relative humidity in hourly intervals and at a spatial resolution of 15 km². Solar radiation and relative humidity were averaged to annual mean values. Altitudinal data were taken from WorldClim (Hijmans et al. 2005), which provides interpolated climate and elevation surfaces, with a spatial resolution of 30 arc seconds. For each grid cell, the environmental data were averaged over a 25 km radius from the centroid using the R-package raster (Hijmans et al. 2016). To alleviate the effects of measurement units with different ranges, mean environmental variables were z-transformed, i.e. the overall mean was calculated and subtracted from the value of each grid cell, and the resulting number was divided by its standard deviation.

Statistical analysis

All statistical analyses and calculations were conducted in R version 3.3.2 (R Core Team 2016). For the complete data set, diurnal subset, and nocturnal subset, the following procedure was applied. First, color lightness values of all species occurring within each grid cell were averaged to obtain one value that represented the species list recorded for each grid cell. Second, we calculated multiple ordinary least-squares (OLS) models with latitude and elevation as independent variables to test for spatial patterns in the color lightness of assemblages. As the standard error of the calculated mean color lightness of assemblages differs in relation to the number of species recorded within grid cells, the models were weighted by the number of species per grid cell. Third, we calculated OLS models with color lightness as the response variable and the environmental variables humidity and solar radiation and their interaction as predictor variables. These models were also weighted by the number of species per grid cell.

Patterns in the geographical variation of traits can occur as a side effect of the proximity of the ranges of species. For example, neighboring grid cells often share the same species. This spatial autocorrelation – the non-independency of closely located grid cells driven by their proximity – violates the assumptions of standard linear models. We evaluated the spatial autocorrelation structure of the residuals of the regression models with spatial correlograms generated with the R-package pgirmess

(Giraudoux et al. 2018). From these spatial correlograms, we estimated the distance after which the effect of spatial similarity was no longer significant for each data set separately (Figs. 9.1.4, 9.1.5, 9.1.6). These distances were used in spatial simultaneous autoregressive models (SAR) in the R package spdep (Bivand et al. 2018), which fits a spatial dependency weight to the error term (Kissling and Carl 2008). The relative importance of single variables was assessed based on their standardized regression coefficients. We also applied null model analyses to verify the robustness of the results (chapter 9.1).

Multi-species data sets violate the assumption of independent variation of traits, as closely related species probably share a phylogenetic component within the trait phenotype (Webb et al. 2002). Hence, patterns in traits such as color lightness could be a result of a structural shift in faunal composition (e.g. Brehm and Fiedler 2004). Unfortunately, the DNA sequences available are not sufficient to generate a well-resolved phylogeny for the numerous species used in this study. Even the most up-to-date phylogeny presented by Holm et al. (2016) covers only 50% of the genera of this study. We therefore chose to repeat the analysis described above for the two largest monophyletic subfamilies (Larentiinae and Sterrhinae, comprising 63% and 31% of the complete data set, respectively), to evaluate whether the results are consistent within these subfamilies (see chapter 9.1).

Results

Color-lightness patterns

Color lightness of species ranged from 0.27 (*Baptria tibiale*) to 0.96 (*Scopula subpunctaria*), with a mean of 0.69 and a standard deviation (SD) of 0.12 (Fig. 9.1.11). Nocturnal and diurnal species did not differ in their color lightness (Welch two-sample t-test, $t = -1.40$, d.f. = 189, $P = 0.16$, Appendix S1, Figure S1.1). The average color lightness of Geometridae assemblages ranged from 0.60 to 0.74 (mean 0.66 ± 0.03 SD, Appendix S7, Figure S7.12). Assemblages of nocturnal moths were slightly lighter colored (mean 0.68 ± 0.03 SD) than assemblages of diurnal moths (mean 0.67 ± 0.03 SD; paired t-test: $t = -19.3$, d.f. = 3613, $P < 0.001$). In the complete Geometridae data set, the average color lightness of assemblages decreased with increasing latitude and elevation (OLS model, $R^2 = 0.67$, Table 4.1.1), with predominantly dark-colored species occurring in Scandinavia and in alpine regions, and predominantly light-colored species occurring in the Mediterranean (Fig. 4.1.1).

TABLE 4.1.1. Results of spatial regression models. Given are regression coefficients and their standard errors. In simple linear regressions, color lightness of moth assemblages was the dependent variable and latitude and elevation were independent variables. Note that color lightness increased with latitude and decreased with elevation in all data sets.

Taxon	Variable	Estimate	± SE	t-value	*P*-value	R^2
Geometridae	Intercept	8.17E-01	1.80E-03	453.1	< 0.001	0.67
	Latitude	−2.77E-03	3.14E-05	−88.21	< 0.001	
	Elevation	−1.97E-05	8.19E-07	−24.12	< 0.001	
Diurnal moths	Intercept	8.00E-01	2.58E-03	310.2	< 0.001	0.48
	Latitude	−2.65E-03	4.50E-05	−58.95	< 0.001	
	Elevation	−1.82E-05	1.17E-06	−15.5	< 0.001	
Nocturnal moths	Intercept	8.62E-01	2.24E-03	384.4	< 0.001	0.70
	Latitude	−3.65E-03	3.97E-05	−91.91	< 0.001	
	Elevation	−2.65E-05	9.76E-07	−27.15	< 0.001	

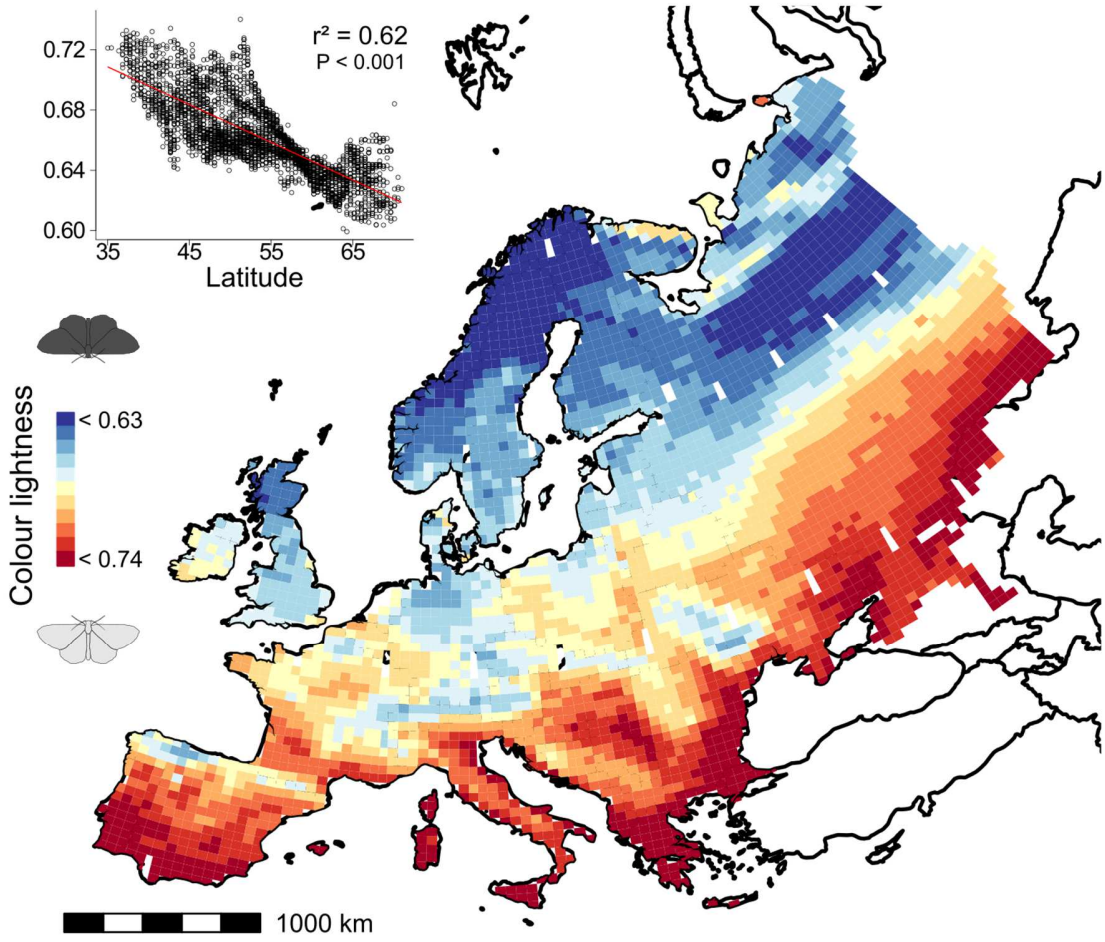

FIGURE 4.1.1. Mean color lightness of assemblages of geometrid moths across the Western Palearctic (637 species in 3,777 grid cells). The color coding represents quantiles, ranging from 0 (black) to 1 (white), with blue indicating dark coloration and red indicating light coloration (Lambert azimuthal equal-area projection). Note that dark-colored species predominantly occur in northern regions and light-colored species predominantly occur in southern regions. Values of r^2 and *P* are from an ordinary least-squares regression with average color lightness within assemblages as dependent variable and latitude as independent variable.

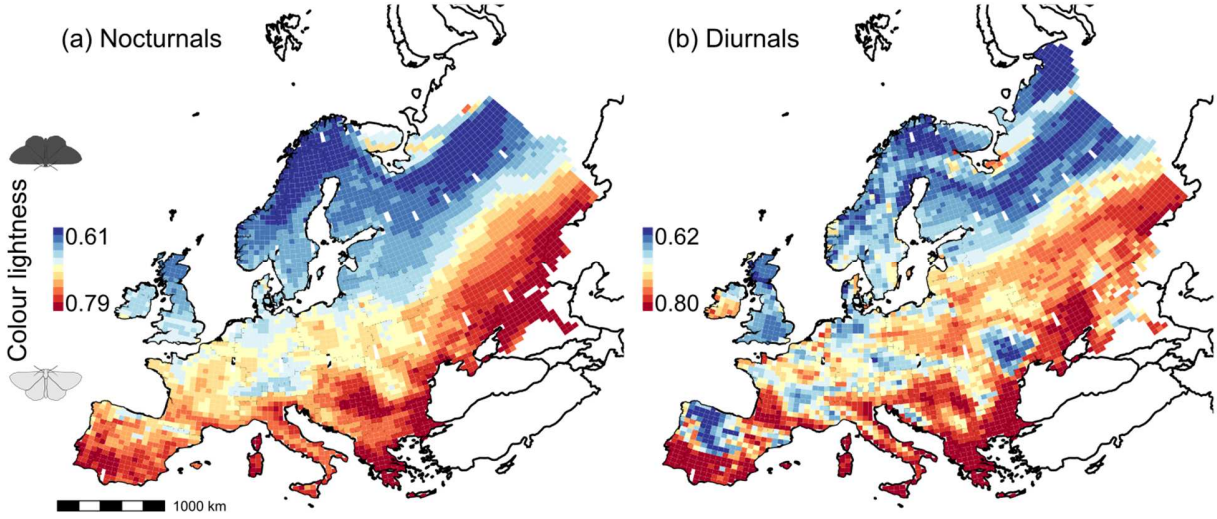

FIGURE 4.1.2. Mean color lightness of subsets of assemblages of geometrid moths across the Western Palearctic. **a)** Strictly nocturnal species (160 species, 3,614 grid cells) and **b)** diurnal species (109 species, 3,775 grid cells). The color coding represents quantiles ranging from 0 (black) to 1 (white), with blue indicating dark coloration and red indicating light coloration (Lambert azimuthal equal-area projection). For both subsets, dark-colored species predominantly occur in northern regions and light-colored species predominantly occur in southern regions.

TABLE 4.1.2. Results of environmental regression models with color lightness as the dependent variable. Given are the estimated coefficients of the ordinary least-squares (OLS) models weighted by the number of species per grid cell, and spatial simultaneous autoregressive (SAR) models. R^2 values of the SAR models are based on Nagelkerke. Note that solar radiation had the highest relative importance (z-value) within all subsets.

	Model	Variable	Estimate	± SE	z-value	*P*-value	AIC	R^2
Geometridae	OLS[1]	Radiation	1.57E-02	4.00E-04	40.8	< 0.001		
		Humidity	−8.10E-03	4.00E-04	−21.2	< 0.001	−21640	0.69
		Radiation:Humidity	3.40E-03	2.00E-04	15.4	< 0.001		
	SAR[2]	Radiation	1.85E-02	6.00E-04	29.9	< 0.001		
		Humidity	−2.10E-03	4.00E-04	−4.99	< 0.001	−22969	0.80
		Radiation:Humidity	−2.00E-04	2.00E-04	−0.76	0.448		
Diurnal moths	OLS[1]	Radiation	1.79E-02	6.00E-04	31.9	< 0.001		
		Humidity	−3.90E-03	6.00E-04	−7.06	< 0.001	−18944	0.46
		Radiation:Humidity	3.40E-03	4.00E-04	9.31	< 0.001		
	SAR[2]	Radiation	2.13E-02	9.33E-04	22.8	< 0.001		
		Humidity	6.78E-04	6.30E-04	1.08	0.282	−19387	0.59
		Radiation:Humidity	4.39E-04	3.83E-04	1.15	0.252		
Nocturnal moths	OLS[1]	Radiation	1.86E-02	5.00E-04	41.3	< 0.001		
		Humidity	−9.80E-03	4.00E-04	−21.8	< 0.001	−19628	0.66
		Radiation:Humidity	7.00E-03	3.00E-04	26.6	< 0.001		
	SAR[2]	Radiation	1.48E-02	7.00E-04	22.4	< 0.001		
		Humidity	−6.70E-03	5.00E-04	−14.0	< 0.001	−21168	0.83
		Radiation:Humidity	2.60E-03	3.00E-04	9.96	< 0.001		

This pattern was found for both nocturnal (R^2 = 0.70) and diurnal (R^2 = 0.48) species assemblages (Table 4.1.1; Fig. 4.1.2 a,b). In the largest monophyletic subfamily (Larentiinae), color lightness of assemblages also decreased with increasing latitude and elevation, but the relationship was notably weaker than in all Geometridae (R^2 = 0.42). By contrast, latitude and elevation explained only 2% of the variation in the color lightness of assemblages of Sterrhinae (chapter 9.1).

Color lightness and environment

The color lightness of assemblages of geometrid moths significantly increased with solar radiation, which had the highest relative importance (viz. large standardized regression coefficient) within both the OLS and the SAR models. The color lightness of assemblages of geometrid moths decreased with increasing humidity, which had the second highest relative importance (Table 4.1.2). The interaction term between solar radiation and humidity was positive within the OLS model, i.e. the positive effect of solar radiation on color lightness increased under high levels of humidity. Within the SAR model, however, the interaction between solar radiation and humidity was not significant (Table 4.1.2).

The color lightness of both nocturnal and diurnal moth assemblages increased with solar radiation and decreased with humidity. Again, the positive regression coefficient of the interaction terms indicated that high levels of humidity increased the positive effect of solar radiation on color lightness. For nocturnal moth assemblages, these relationships were also observed in the SAR model, whereas for diurnal moth assemblages, only solar radiation remained a significant explanatory variable (Table 4.1.2). The null model analysis described in chapter 9.1 largely confirmed our results. Solar radiation was consistently positively correlated to color lightness within the two monophyletic subfamilies, whereas humidity showed contrasting effects. The interaction term was negatively correlated to color lightness in both subfamilies (chapter 9.1).

Discussion

In this study, we investigated the relative importance of humidity and solar radiation on the color lightness of diurnal and nocturnal geometrid moth assemblages across the Western Palearctic. We assumed that the relative importance of dark or light coloration for thermoregulation is considerably lower for nocturnal species than for diurnal species and hence that macroecological patterns in their color lightness is predominantly shaped by the protection from pathogens and UV radiation provided by melanin. In contrast to our expectations, however, both diurnal and nocturnal groups showed a distinct concordant gradient in color lightness ranging from light-colored assemblages in the Mediterranean basin to dark-colored assemblages in northern Europe and north-western Russia. We also found similar trends towards more dark-colored assemblages at high elevations, e.g. in the Alps, Pyrenees and Carpathians. These declines in color lightness with latitude and elevation are reflected in the overall geographical pattern of geometrids of the Western Palearctic. Strikingly, this geographical variation in color lightness strongly resembles the outlined pattern expected if only thermoregulatory functions of dark or light coloration were of importance, as has been discussed with regard to heliophilic insects, such as butterflies and dragonflies (Zeuss et al. 2014, Pinkert et al. 2017).

Assuming that the risk of infection by pathogens is generally higher under warm (Yin et al. 2016) and/or humid conditions (Reilly et al. 2014), and assuming that darker coloration is indicative of higher immuno-competence (Wilson et al. 2001) we expected color lightness to negatively co-vary with relative humidity and solar radiation. Moreover, we expected that the protective function of dark coloration against pathogens is more important for nocturnal moths than for diurnal moths. In fact, we found that humidity had no effect on the color lightness of diurnal species after accounting for spatial autocorrelation, whereas humidity had a negative effect on color lightness of nocturnal species. However, the effect of humidity on color lightness was not consistent across monophyletic subfamilies and should thus be interpreted with caution. Moreover, the negative effect of humidity decreased with increasing radiation, as indicated by the positive sign of the regression coefficient of the interaction term in our models, i.e. assemblages were on average not darker colored in warm and humid environments (Table 4.1.2). The converse argument suggests that nocturnal species assemblages tend to be darker in cold and humid environments. However, the positive relationships between solar radiation and color lightness by far exceeded the observed contingencies with humidity, leaving solar radiation as the most important driver for the observed geographical variation in color lightness on the macroscale.

The consistent increase in color lightness with increasing solar radiation throughout all data sets contradicts the hypothesis that UV protection is the major driver for the variation in color lightness of assemblages. However, we cannot disentangle effects of temperature and UV radiation in the context of this macroecological study. Thus, the protection against UV radiation might still be of importance at high elevations, where assemblages were on average darker colored (Table 4.1.1). Both the increase in color lightness in warm areas (low latitudes and elevations) and the decrease in color lightness in areas with high UV radiation (high elevations) were similar to the findings of Bishop et al. 2(016), who suggested that thermoregulation and protection against UV radiation can simultaneously influence insect color lightness. Nevertheless, our results clearly demonstrate that protection against UV radiation is not the dominant process shaping macroecological patterns in insect color lightness across the Western Palearctic.

Given that our results do not indicate that protection against UV radiation or pathogens is the most important function of color lightness in geometrid moths and that thermal melanism should not extend activity periods of nocturnal insects, the most important question arising from our study is why does solar radiation have such a strong positive correlation with the color lightness of nocturnal moths? We see three possible reasons for this mismatch between our predictions and findings. First, thermal benefits gained from the absorption of solar radiation might not be restricted to periods of activity, but might also positively affect physiological processes during the resting phase. In line with this reasoning, Ellers and Boggs (2004) observed that immobilized dark-colored females of *Colias* butterflies had accelerated egg maturation rates compared to light-colored ones under a given level of solar radiation. Yet, during rest, a low body temperature might be more advantageous because more energy resources are conserved (Heinrich 1993). Second, insects that are nocturnal as adults might be diurnal as larvae, and hence might benefit from thermal melanism in terms of increased activity during

earlier life stages (e.g. Davis et al. 2005, Karl et al. 2008). If upregulation of melanin synthesis is retained across different life stages, the geographical pattern of color lightness that we found might result from thermal melanism of diurnal larvae. At the moment, however, transitions in insect traits from juveniles to adults are poorly understood (Pechenik 2006). Moreover, although thermal melanism has already been observed in larvae of moths (Goulson 1994, but see Välimäki et al. 2015), the larvae of geometrid moths are more likely to be thermoconformers than active thermoregulators (Heinrich 1993). Third, color lightness has been shown to be correlated to other morphological and developmental traits, which are themselves temperature dependent. These correlations might be based on genetic coupling or trade-off relationships between the investment in melanin and e.g. body size, development time or clutch size (True 2003, Suzuki and Nijhout 2008, Mckinnon and Pierotti 2010). For example, Talloen et al. (2004) found that dark-colored speckled wood butterflies had longer development times, which are usually associated with low temperatures (Sibly and Atkinson 1994). Hence, the observed decrease in color lightness of nocturnal moths with decreasing solar radiation might result from longer development times at low temperatures (e.g. Zeuss et al. 2017; but see Prokkola et al. 2013). More research is needed to elucidate whether thermal melanism is also beneficial during the resting phase of nocturnal insects and whether the observed macroecological patterns in adult color lightness are a result of thermal melanism during earlier life stages or due to linkages to temperature-dependent morphological and developmental traits.

In summary, our study showed that the geographical patterns of color lightness of nocturnal and diurnal insects are broadly similar. Although UV radiation might be an important factor at high elevations and the relative importance of humidity was higher for nocturnal species, the thermal environment appears to be the most influential climatic driver of insect color lightness – independent of thermoregulatory strategy and nocturnal or diurnal activity. In any case, the very existence of strong positive correlations between color lightness and the thermal environment among diurnal and nocturnal insects, such as reported in this study, challenges the view that extended periods of activity mediated through thermal melanism are the main driver of geographical variation in insect color lightness. As a consequence, the relationship between insect color lightness and the thermal environment might be even more general than previously thought.

Acknowledgments

D.Z. is supported by a PhD scholarship from Evangelisches Studienwerk Villigst, funded by the German Federal Ministry of Education and Research. We thank Karen A. Brune for improving the text linguistically. Special thanks go to Roman Fricke for comments on an earlier version of the text.

Chapter 4.2

A local elevational gradient in the body size and color lightness of nocturnal insects: contrasting strategies among noctuid and geometrid moths

with

Lea Heidrich | Stefan Pinkert | Nicolas Roth | Jörg Müller | Roland Brandl |

first draft in preparation for submission to *Functional Ecology*

This paper is a follow-up on the previous chapter and was initiated by the fruitful discussions of Lea Heidrich and me, which led to the idea of this study. Here, Ms. Heidrich supported me strongly during the field work in the Bavarian Forest National Park. The conceptual framework of this first draft, the analyses therein and the major conclusions are predominantly my personal contribution.

Summary

Trait-environment relationships are crucial for the prediction of community responses to environmental change. As ectothermic organisms completely rely on external heat sources, traits which alter the uptake or maintenance of external heat should have direct effects on species performance, especially in cold environments. In this study we investigate the relationship between two traits relevant for thermoregulation – namely body size and color lightness – with changing thermal environment along an elevational gradient in Southern Germany. Here, we analyze data on 17,560 individuals of 211 species of nocturnal moths (Lepidoptera) from the families of Geometridae and Noctuidae from 33 forest sites sampled in the years 2007 and 2016. Assemblage-level models of community-weighted trait means, species-level models of species' abundances and fourth-corner analyses consistently revealed contrasting strategies for both moth families. Moths from the family Geometridae showed no or only weak trait-environment relationships and geometrid abundance was most strongly affected by local environmental conditions, namely habitat availability. Moths from the family Noctuidae showed strong trait-environment relationships with larger and darker moths outperforming smaller and lighter moths at high elevations. These results are discussed in the context of the different flight behaviors and resulting energetic requirements of geometrids and noctuids as well as in the context of recent empirical results at larger spatial scales. Overall, our study shows that trait-environment relationships are highly context dependent and not scale-invariant, with large variation even amongst closely related taxa. Thus, for a reliable assessment of the vulnerability of organisms to environmental change we need a well-grounded knowledge of trait-environment relationships across and among taxa, as well as of the variation in the strength and direction of these relationships in space and time.

Introduction

By definition, functional traits affect species' performances in terms of growth, fecundity or survival depending on environmental conditions (McGill et al. 2006, Violle et al. 2007). Such trait-environment relationships enable ecologists to identify which species will be selected from a species pool in a given environment (Keddy 1992). A generalization of trait-environment relationships may further facilitate predictions on community responses, e.g. in terms of changes in the relative abundance of species, to environmental change (Laughlin and Messier 2015). Species performance is inherently dependent on the metabolic rate of an organism as it determines the rate of energy uptake and expenditure (Enquist et al. 1998, 2015). For ectotherms, which completely rely on external heat sources in order to uphold body temperatures sufficient for activity, traits which alter the uptake or maintenance of external heat should have direct effects on species performance.

Given that the metabolic rate of a species is a function of its body mass and temperature (Brown et al. 2004), species' body sizes are often the focus of trait-based approaches (e.g. Horne et al. 2015, Zeuss et al. 2017). As larger bodies reach higher equilibrium temperatures than smaller ones (Atkinson 1994), species should show phenotypic differentiation in terms of body size along temperature gradients, with larger bodies being beneficial in colder environments. Yet, the body size of ectotherms, especially insects, is constrained by for instance energetic requirements or development times associated with larger bodies (e.g. 'temperature size rule', (Atkinson and Sibly 1997) resulting in

ambiguous empirical evidence for relationships of body size with temperature (Shelomi 2012).

Another possibility for small organisms to reach high performances in cold environments are adaptations related to improved thermoregulation in terms of heat retention or heat absorption. Such adaptations may include the color lightness of species' cuticles. With all else being equal, darker organisms heat up faster and attain higher equilibrium body temperatures than their light-colored counterparts at a given level of solar irradiance (e.g. Watt 1968). Thus, the thermal melanism hypothesis (TMH) states that being dark should be beneficial in colder environments (Clusella Trullas et al. 2007). In recent years the TMH received empirical support based on studies along elevational and latitudinal gradients for diurnal, flying insects such as odonates and butterflies (Ellers and Boggs 2004, Zeuss et al. 2014). Moreover, in a previous study we found that the mean color lightness of nocturnal geometrid moth assemblages decreases with increasing latitude and decreasing temperature (Heidrich et al. 2018). As we assumed that nocturnal insects would not benefit strongly from increased absorption of solar irradiance due to their activity period, this study implied that the TMH might be more general than previously formulated but also illustrates that the underlying effects on the performance of species are not as fully understood as previously thought (see also Umbers et al. 2013).

It is a premise of trait-based ecology that the effect of traits which link the environment to performance can be scaled up from an individual to the ecosystem (Enquist et al. 2015). However, the question arises whether the thermal environment acts as a selective pressure for insect color lightness and/or body size on smaller spatial and temporal scales, on which the importance of temperature as selective force is likely to decrease, while the importance of biotic drivers, such as local resource availability, increases (Schweiger and Beierkuhnlein 2015) Given for example the high multifunctionality of color lightness (True 2003), it is necessary to evaluate whether predictions based on large-scale variations in color lightness can be transferred to smaller-scales and *vice versa*.

In this study we aim to investigate how the body size and color lightness of nocturnal moths affects species performances on a local scale. Therefore, we sampled moth assemblages of the families Noctuidae and Geometridae using light-traps along an elevational gradient in South Eastern Germany in 2007 and 2016.

Here, we test the hypotheses that (i) the mean body size of moth assemblages increases with increasing elevation and (ii) the mean color lightness of moth assemblages decreases with increasing elevation. Furthermore, as we expect that larger or darker bodies are beneficial at higher elevations we predict that (iii) darker and/or larger species are more abundant at high elevations than lighter and/or smaller species (i.e. a significant interaction term of body size or color lightness with elevation).

Methods

Study area

The study was conducted at the Bavarian Forest National Park in the German part of the Bohemian Forest in south-eastern Germany. Sampling sites were established along an elevational gradient of 660 to 1368 m a.s.l. at 33 forest sites in 2007 and resampled in 2016. Up to 1150 m a.s.l. the National Park is dominated by a mixed mountain forest of spruce *Picea abies*, European beech *Fagus sylvatica*, and fir *Abies alba*. Above

1150 m a.s.l. spruce dominates with low proportions of mountain ash *Sorbus aucuparia* and European beech.

Sampling

Moths were sampled monthly from June to August using light-traps at nights with optimal weather conditions (i.e. no sampling with rainy conditions or during full moon) resulting in 99 samples for 2007 and 2016 respectively. Light traps consisted of 12V and 15W superarctinic UV-lights linked to a twilight-sensor and powered by a 12V, 15Ah Battery. The catch was collected the next day and subsequently frozen before the determination to the species level. Overall catchments included 21,679 individuals of 273 species belonging to 10 families.

Morphological traits

As a proxy for species body size we used recently published information on species' wing spans (henceforth 'body size'; Potocký et al. 2018).

In order to quantify color lightness for the species under study we scanned photographs of museum specimens published as colored plates in '*The Macrolepidoptera of Germany'* (Segerer et al. 2011), which includes 6171 images of 1377 species. Colored plates were scanned using a Scanner at 300 dpi with RGB color space. For each species, we extracted the images and removed the background. For each image we then averaged grey values of all pixels, using the package *png* (v. 0.1-7; Urbanek 2013) in the *R* environment (v. 3.4.2; R Core Team 2017). Mean grey values were averaged over all images available for a species resulting in one value of color lightness for each species ranging from 0 (all black) to 100 (all white).

Habitat availability

In order to account for variations in resource availability, we included information on the occurrence of larval host plants into the analysis. For all species in our study region information on most frequent host plants is available in the literature (e.g. Pearse and Altermatt 2013, Steiner et al. 2014). At all study sites the coverage of plant species was estimated within a radius of 8 m around the center of the site (approximately 200 m²) at four vertical layers (i.e. >15 m; >5-15 m; >1-5 m and <1 m). For coverage estimation a modified decimal scale after Londo (1976) was used. Percentages of all layers were summed and divided by the number of layers followed by a logit transformation in order to achieve normality.

Statistical analysis

As morphological traits generally display strong phylogenetic signals we decided to perform all analyses separately for two subgroups, namely the families of Geometridae and Noctuidae. Specimens of both families account for 81 % of all individuals of our total catchment and occur in comparable magnitudes with 11,459 individuals of 109 species of Geometridae and 6,101 individuals of 102 species of Noctuidae.

For each site in both years we calculated community weighted means of body size and color lightness. Here, the trait value of a species was weighted according to its abundance at the site. We calculated linear models of the community weighted trait means with elevation and year and the interaction of elevation and year as predictor variables.

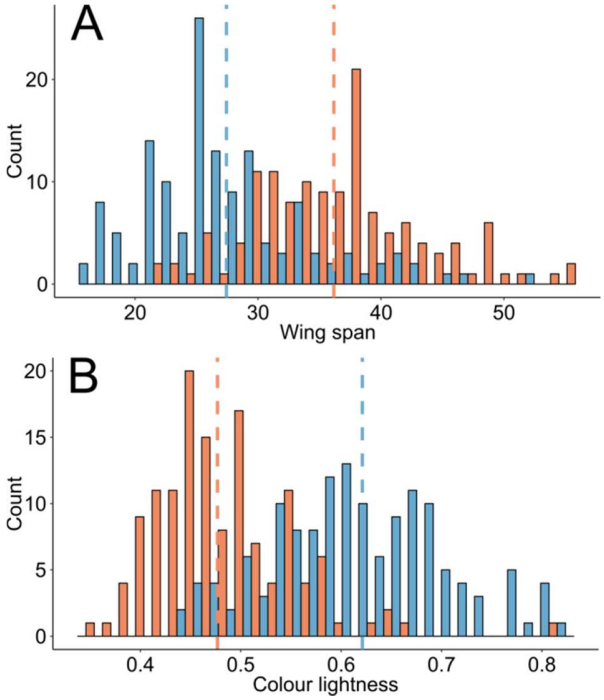

FIGURE 4.2.1. Histogram of trait values of moth species of the families Geometridae (blue) and Noctuidae (red). (A) Body size as wing span in millimeters. (B) Color lightness ranges from 0 (black) to 1 (white).

In the species-level analysis we modelled the abundance of the species with generalized linear mixed models as implemented in the glmmTMB package (Brooks et al. 2017). Here, we used a poisson error distribution with a log-link function and an observation-level random effect. With the observation-level random effect we can account for frequently observed overdispersion in models of count data (Harrison 2014). The models furthermore included species' genera and identities as a nested random effect in order to account for non-random differences between species such as phylogenetic relatedness. Species' abundances were predicted by the interaction between the linear and the quadratic term of elevation and species traits, as well as an interaction term of elevation and species' habitat availability.

TABLE 4.2.2. Results of the species-level analysis. Models were calculated with assuming a poisson error distribution and including an observation-level random effect, as well as a nested random effect including taxonomic genus and species' identity. The 'best' model was determined via lowest AIC. For the averaged model all models with ΔAIC below 3 were averaged.

	Geometridae			Noctuidae		
Predictor	Full model	Best model	Averaged model	Full model	Best model	Averaged model
Elevation	-1.84	-1.70	-1.46	**-3.32**	**-3.22**	**-3.13**
Elevation²	-1.83	**-2.14**	-1.80	**-2.24**	**-2.22**	**-2.10**
Body size	1.41	1.54	1.76	0.93	1.05	1.02
Body size * elevation	-0.68	-	-0.94	**2.91**	**2.97**	**2.92**
Body size * elevation²	-0.27	-	-0.41	0.01	-	0.02
Color lightness	-1.40	-1.46	-1.54	1.15	1.27	1.13
Color lightness * elevation	0.53	-	1.02	**-3.19**	**-3.07**	**-3.16**
Color lightness * elevation²	0.37	-	0.72	**-2.48**	**-2.68**	**-2.51**
Habitat availability	**4.30**	**4.72**	**4.36**	0.29	-0.55	-0.21
Habitat availability * elevation	-1.53	**-1.98**	-1.55	**-2.08**	**-2.20**	**-2.15**
Habitat availability * elevation²	-1.44	-1.77	-1.32	-1.10	-	-1.09
Year	0.40	-	0.44	0.69	-	0.69
Marginal R^2	0.07	0.07	-	0.05	0.05	-
Conditional R^2	0.24	0.24	-	0.25	0.25	-

TABLE 4.2.1. Results from linear regressions of community weighted means of body size and color lightness for Geometridae and Noctuidae moths.

Family and response	elevation	year	R^2
Geometridae			
Mean body size	-1.34$^{n.s.}$	-1.12$^{n.s.}$	0.04
Mean color lightness	**2.32***	0.63$^{n.s.}$	0.08
Noctuidae			
Mean body size	**7.65*****	-1.56$^{n.s.}$	0.48
Mean color lightness	**-6.88*****	**3.99*****	0.49

Furthermore, the models included the sampling year as a fixed effect. We first calculated the full model, followed by a dredging and averaging procedure based on AIC as implemented in the MuMIn package (Grueber et al. 2011, Barton 2015). All models with a difference in AIC values equal to or below 3 were included in the model averaging procedure. We discuss the results of the full model, the top model and the averaged model.

In order to directly test the trait-environment interaction between elevation and species traits we performed a fourth-corner analysis as implemented in the ade4 package (Dray and Dufour 2007). For this we used the species-site matrices for both families in both years, a matrix of site-level elevations, as well as a matrix of species-level trait values. The fourth-corner statistic measures the link between those three matrices and allows inference about an unknown 'fourth corner', the trait-environment interaction matrix (Dray and Legendre 2008, Braak et al. 2012). The link between trait and environment is measured as a Pearson correlation coefficient with its significance being tested by a permutation procedure. Here, we permute both site and species values and combine both outputs as other procedures are prone to inflated type I statistical errors (Dray and Legendre 2008, Braak et al. 2012).

Results

Wing spans ranged from 16 mm (*Eupithecia tenuiata*, Geometridae) to 55 mm (*Eurois occulta*, Noctuidae) with a mean of 31.7 mm ± 8.1 mm (mean ± standard deviation). Here, noctuids had on average 8.7 mm larger wing spans than geometrids (ANOVA: $F_{1,274} = 111.4$, $P < 0.001$, $R^2 = 0.29$; Fig. 4.2.1A). Color lightness values ranged from 0.34 (*Noctua janthina,* Noctuidae) to 0.82 (*Scopula immutata,* Geometridae) with a mean of 0.55 ± 0.11. Moths from the family of Noctuidae were on average 0.14 percentage points darker than species from the family of Geometridae ($F_{1,274} = 239.4$, $P < 0.001$, $R^2 = 0.46$; Fig. 4.2.1B).

The assemblage-level models revealed strong differences in mean trait values of the two families in response to increasing elevation. Mean body sizes of noctuid assemblages increased with increasing elevation (Table 4.2.1; Fig. 4.2.2). Mean body sizes of geometrid assemblages did not change with increasing elevation (Table 4.2.1; Fig. 4.2.2). Mean color lightness of noctuid assemblages decreased with increasing elevation (Table 4.2.1; Fig. 4.2.2). For geometrid assemblages we found a weak increase in mean color lightness values with increasing elevation (Table 1; Fig. 2).

The species-level models again revealed strong differences in the response of noctuids and geometrids to increasing elevation. Noctuid species showed strong responses to changing elevation in terms of species' abundances (Table 4.2.2). Furthermore, all models indicated significant trait-environment interactions with darker and larger species being more abundant at high elevations (Table 4.2.2).

TABLE 4.2.3. Results from the fourth corner analysis for Geometridae and Noctuidae for both years 2007 and 2016. Significance of the fourth corner statistic determined via permutation of site and species values based on 9999 permutations.

	Geometridae		Noctuidae	
Year	2006	2016	2006	2016
Elevation * body size	-0.05^{ns}	-0.02^{ns}	**0.32***	**0.32***
Elevation * color lightness	0.10^{ns}	0.02^{ns}	**-0.37.**	**-0.28***

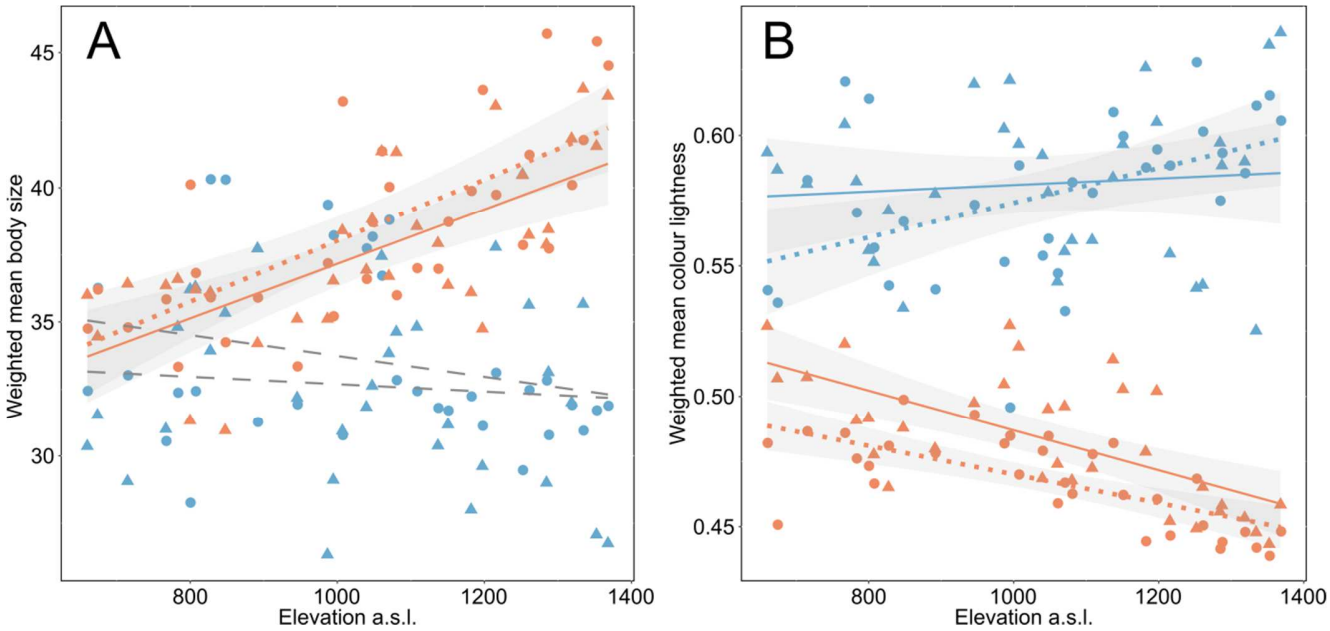

FIGURE 4.2.2. Community weighted trait means for assemblages of Geometridae (blue) and Noctuidae (red) along elevation above sea level in the years 2007 (dotted line and circles) and 2016 (continuous line and triangles). Species trait values in the assemblage were weighted according to species' abundances. The grey area corresponds to the 95 % confidence interval of a linear regression. (A) Community weighted mean of body sizes. Note that for species of the family of Geometridae the relationship between mean body size and elevation was non-significant in both years (dashed grey line). (B) Community weighted mean of color lightness values.

Geometrid species on the other hand did not show a strong response to changing elevational conditions in terms of abundance. Most notably, morphological traits did not affect species abundances in interaction with elevation (Table 4.2.2). The most important predictor for the abundance of geometrid moths was the availability of host plants at the study site (Table 4.2.2).

The fourth-corner analysis largely confirmed the results of the previous analyses (Table 4.2.3). For noctuids we found significant trait-environment interactions of body size and color lightness with elevation, while none was found for geometrid moths. These results were robust over both study years (Table 4.2.3).

Discussion

The results of this study revealed three important aspects: (1) there is a significant trait-environment relationship between elevation and both functional traits body size and color lightness affecting species' performances in terms of abundance; (2) moths of the families Noctuidae and Geometridae display divergent strategies along the elevational gradient and (3) the pattern of decreasing color lightness with decreasing temperature found on a continental scale could not be confirmed on a local scale for geometrid moths.

As shown in several studies, species' morphology has the potential to facilitate individual performance along elevational gradients (Tiede et al. 2018). An increase in mean body size with elevation was recently shown in tropical moth assemblages along a complete elevational gradient (Brehm et al. 2018).

The overall evidence is however ambiguous with other studies showing negative or no relationship of body size with elevation at all (Brehm and Fiedler 2004, Shelomi 2012). In our study, the family of Noctuidae showed a decrease in community weighted means of body size with elevation, an increase in abundance of large species at higher elevations and a significant trait-environment relationship based on fourth corner analysis. Here, all results are in accordance with the expectations for a response to a decrease in environmental temperature with increasing body size. Moths of the family of Geometridae on the other hand showed no relationship of body size with elevation at all, reflecting the ambiguity of the evidence in the literature on body size-elevation relationships. Here, body size did not affect the abundance of geometrid moths and no trait-environment interaction was apparent in the fourth corner analyses. The results for color lightness point in a similar direction, with assemblages of Noctuidae displaying a strong decrease in mean color lightness and a distinctive trait-environment interaction of color lightness and elevation on the species level. Geometridae on the other hand showed a weak increase in community weighted mean color lightness with elevation and no apparent trait-environment interaction. At the same time, the amount of available habitat in the surrounding had no effect on the abundance of noctuid species, while it was the most important driver of abundance for geometrid species. These results suggest that on the scale under study noctuid moths are more strongly affected by the thermal environment, while geometrid moths are more dependent on high densities of their host plants.

The results are especially surprising for geometrid moths, as our previous study across continental Europe showed a strong decrease of mean color lightness with increasing latitude (Heidrich et al. 2018, Xing et al. 2018). Furthermore, a recent study at a smaller spatial scale

found a decrease of mean color lightness with increasing elevation, most pronounced in the subalpine zone of Yunnan, China (Xing et al. 2018) This underlines the fact that ecological and evolutionary mechanisms act on different scales and are highly context specific and one cannot necessarily infer local scale processes from macroecological observations or generalize results from a particular regions to others (Grime 2006, Enquist et al. 2015, Pearse et al. 2018). In the aforementioned study in continental Europe, we found strong differences in the spatial pattern of mean color lightness among the subfamilies of Geometridae, namely Sterrhinae and Larentiinae and a recent study on Andean butterfly communities revealed diverging patterns among two closely related genera (Dufour et al. 2018, Heidrich et al. 2018). Species' strategies to cope with environmental gradients are apparently variable at least in Lepidopterans and may be highly context dependent (see also Stelbrink et al. 2019). Additionally, large-scale patterns may rather reflect species co-occurrences leading to patterns that are not scale-invariant with limited applicability for local-scale predictions (Hawkins et al. 2017).

In the case of our study system both families differ quite strongly in their ecology. Geometrid moths have relatively larger wings, smaller bodies and thus significantly lower wing loading and stroke frequencies compared to noctuid moths (Casey and Joos 1983). Thus, geometrid moths fly with low energetic costs, which allows them to be active over a wide range of temperatures, though their flight performance is relatively poor ("cool moths", Utrio 1995). In contrast, noctuid moths are capable of rapid flight and hovering, but must raise their body temperatures above ambient temperatures in order to take off ("hot moths", Utrio 1995). This pre-flight warm up, together with high wing load, is energetically costly, especially if ambient temperatures are low (Casey and Joos 1983).

Our study revealed two strongly divergent strategies among two closely related insect families in terms of trait-environment interactions. This implies that in the context of environmental change like the inevitable warming of environmental temperatures; even closely related species might display strong differences in their response. Furthermore, large-scale observations as in our case for geometrid moths do not warrant that the same patterns and processes take place at smaller spatial scales. Thus, for a reliable assessment of the vulnerability of organisms to environmental change we need a well-grounded knowledge of trait-environment relationships across and among taxa, as well as of the variation in the strength and direction of these relationships in space and time.

Acknowledgments

NF received a scholarship from the Rudolf and Helene Glaser Foundation organized in the "Stifterverband für die deutsche Wissenschaft". We thank Hermann Hacker for the determination of the moth species and Klaus Thiele, Helmut Linhard and Marion Dorsch for the determination of the plant species.

Chapter 5

Conclusion

As global change and associated uncertainties progress, more and more voices are calling for better predictions concerning the future of ecological communities and ecosystems (Palmer et al. 2005, Maris et al. 2018). Ecological systems, however, exhibit a high degree of contingency which led John H. Lawton in his controversial paper 'Are there general laws in ecology' to call community ecology a 'mess' (Lawton 1999). Additionally, the interplay among temporal and spatial scales across all levels of ecological organization further aggravates reliable predictions of the consequences of environmental change (Levin 1992). In the three years of research presented in this thesis, both phenomena – the high level of contingency as well as the problem of scale in ecological communities – become quite apparent. Here, the study of communities along gradients of environmental conditions as space-for-time substitutions as well as the promises of trait-based ecology of generalizability and scalability (Reich et al. 1997, Shipley 2007, Shipley et al. 2016) may shed a light on how communities may respond to ongoing environmental change.

In chapter 2 I presented three studies on community responses to environmental gradients in forest ecosystems. The first study showed the generally strong effect of elevation on alpha-, beta- and gamma-diversity. Here, beta-diversity among elevational zones contributed the largest fraction to overall gamma-diversity in the region (Fig. 2.1.6). This is not surprising as even the rather small elevational gradient of 1000 m in this study is accompanied by a change in temperature comparable to travelling from Rome, Italy to Berlin, Germany. The change in environmental conditions along the elevational gradient contributed to the high degree of beta diversity among forest sites mainly due to species turnover, rather than nestedness. Thus, it is not the mere loss of species due to harsher environmental conditions, decreasing productivity or a decrease in area at the uppermost parts of the mountain ranges that drive this elevational pattern of beta diversity. Furthermore, this study reveals strong differences in the explanatory power of elevation for species turnover among different organism groups, ranging from around 1 % explained variance in bees and wasps to nearly 50 % in beetles (Table 2.1.3). Thus, even among insect orders at the same location sampled during the same period we find strong differences in the relative importance of environmental drivers for their community composition. The second study revealed that changes in forest structure over the course of temperate forest succession affect biodiversity in terms of alpha-diversity. This was mainly by increasing the number of individuals due to an increase in habitat amount. Here, some groups additionally benefited of an increase in habitat heterogeneity. Furthermore, the gradual change in community composition over the course of succession, which largely contributed to regional gamma-diversity, emphasizes the importance of maintaining forest landscapes with appropriate representations of all stages of forest succession. Here, early and late stages of forest succession are currently underrepresented in the forests of Europe (Fig. 7.1.9). While late successional stages have to develop naturally over long time periods, early successional stages may be created artificially by logging or naturally by disturbance events such as wildfires, insect outbreaks or wind throws. The disturbance regime in forests however changed strongly in recent years and is expected to change drastically with ongoing climate change in the coming decades (Seidl et al. 2017, Sommerfeld et al. 2018, Senf et al. 2018). Our study showed that this will inevitably affect the biodiversity and community structure of

forest-dwelling organisms and it remains a central question how the future disturbance regimes and patterns of forest successional stages will affect ecosystem functioning in forests (Ammer et al. 2018). The third study illustrates the contingencies of ecological communities as mentioned by Lawton (1999) quite well, as in contrast to the previous two studies, the arthropod communities in fruiting bodies of *Fomes fomentarius* were only weakly affected by gradients in macroclimatic and forest structural conditions (Figure 2.3.4). This was despite the fact that the environmental gradient especially in terms of climate was even larger than in the previous study, covering e.g. mean climatic conditions ranging from Spain to Sweden (Figure 2.3.1). Here, the perennial bracket fungus apparently offers similar conditions across large gradients of climate and space and species occurring inside the fruitbodies are less likely to exhibit strong responses to changes in external environmental conditions as long as the occurrence of the fruitbody itself is warranted and dispersal among fruitbodies is possible. As these factors are mostly warranted in landscapes with large proportions of forest patches with old-growth attributes, the fungus-dwelling communities are mostly threatened by regional intensification of forest management. Observational studies as presented in this chapter may help to narrow down taxonomic and functional groups that are most likely to show community-wide responses to environmental change and may capture which aspect of global change will have the strongest effect. Furthermore, the high variability in responses change in macroclimatic conditions and land-use-related habitat conditions may for instance lead to changes in the velocity (e.g. Bässler et al. 2013) or the direction (e.g. Lenoir et al. 2010) of spatio-temporal shifts in species occurrences.

In chapter 3, I presented two studies investigating how species' traits affect species' performances in terms of distribution and abundance. Here, the first study revealed the dynamic nature of the ubiquitous relationship between distribution and abundance of species rejecting hypotheses assuming structural mechanisms (Fig. 3.1.4; Table 3.1.2). In the context of phytophagous insects, the dynamic relationship of distribution and abundance is modulated by the availability of high-quality habitat in the surrounding landscape, which was in accordance with the habitat-dispersal hypothesis (Venier and Fahrig 1996). At the scale under study, species may attain larger distributions if sufficient habitat facilitates the rate and success of dispersal events, which in turn increase local abundance and decrease the probability of local extinction *via* drift. One important aspect of this study was that habitat quality apparently was very important in driving these processes, an aspect often neglected in comparable studies. Interestingly, morphological traits – even those associated with propensity for dispersal – did not affect this relationship. This aspect was central to the second study of this chapter. Here, the causal framework of the first study was maintained including the dynamic relationship of distribution and abundance and the effect of habitat availability on distribution. The second study revealed that the effects of morphological traits on species' performances appear obscured due to energetic trade-offs, as these traits may be beneficial but are energetically costly. This became apparent after the effects of energy uptake and expenditure were included in the confirmatory path analysis of the distribution and abundance of butterflies in Switzerland (Figure 3.2.2.). The study illustrates the importance of the energy budget of organisms in determining vital rates and the potential for an integration of dynamic energy budget

models that might elucidate how the costs of beneficial traits affect vital rates at a given level of available energy (Kooijman et al. 2008, Llandres et al. 2015). The second study, furthermore confirmed the causal framework where habitat availability positively affects species' distributions which in turn facilitates species' local abundance and *vice versa* (Figure 3.2.2). It is indicative that in both studies on phytophagous insects the factor that best represents a trait-environment interaction, namely habitat availability, was the most important predictor modulating the distribution-abundance relationship. Phytophagous organisms exhibit morphological and behavioral adaptations towards the utilization of their host-plant. The number and identities of host-plants may be seen as an integration of the traits of the organisms. At the same time the host-plants are the resource of the organism exhibiting variation in space and time and can be viewed as an environmental condition. If we assume 'eating plant species X' as a trait and 'plant species X occurs in a specific density on a specific site' as an environmental condition, correlating the local host-plant density against the abundance of the associated phytophagous organism is comparable to modelling vital rates as a function of the trait-environment interaction (i.e. '*vital-rates approach'* sensu Laughlin et al. 2018).

In chapter 4, I presented two studies investigating the relationship between the color lightness of nocturnal moths and their thermal environment on small and large spatial scales. The first study revealed a latitudinal decline in the color lightness of assemblages of geometrid moths. Generally, this result was in line with other studies on insect color lightness on comparable scales (e.g. Zeuss et al. 2014). However, as this relationship was previously assumed to be exclusive in heliothermic organisms, these results were still surprising. More interesting, the second study revealed that this relationship of color lightness and the thermal environment of nocturnal geometrid moths is unimportant at a local scale (Figure 4.2.2, Table 4.2.2). This was in contrast to noctuid moths, which showed a strong trait-environment interaction concerning thermoregulatory traits including body size and color lightness. Here, larger and darker species were more abundant at higher elevations and *vice versa*. This study conveyed two important aspects concerning trait-environment relationships. First, trait-environment relationships share the high level of contingencies (Lawton 1999) and the problem of scale (Levin 1992) with all other ecological processes illustrated by the fact that the interaction of the thermal environment and the trait color lightness appears to be strong at large spatial scales and weak at small spatial scales for geometrid moths. Second, trait-environment relationships might vary strongly even among closely related taxa like geometrid and noctuid moths. Both aspects appear in contrast to the generality promised by trait-based approaches.

Two decades after Lawton called community ecology a mess we are still far from general ecological laws that enable us to predict exactly how ecological communities will respond to environmental change. Identifying important environmental gradients driving community dynamics (chapter 2), determining the drivers of species' performances in terms of vital rates (chapter 3) and analyzing the interactive effect of environment and traits on species' performances across scales (chapter 4) as pursued in this thesis helps us to identify the relevant drivers on particular scales for particular communities and species assemblages. Although it is currently not possible to generate reliable and generalizable predictions of how change in terms

of macroclimatic conditions or land-use will affect terrestrial communities as a whole the presented results offer valuable insights on how organisms may interact with their environment. However, as unforeseeable as the future of the conditions surrounding us is at present, nature's response to it will be as unpredictable.

Chapter 6

Deutsche Zusammenfassung

Die wissenschaftliche Ökologie untersucht Organismen in Wechselwirkung mit ihrer Umwelt. Ob und wie erfolgreich ein Organismus überlebt, wächst, sich ausbreitet oder reproduziert hängt von den Merkmalen des Individuums und den Umweltbedingungen ab, mit denen es konfrontiert ist. Das Verständnis der Wechselwirkungen von Artmerkmalen und Umweltbedingungen sowie deren Auswirkungen auf Individuen, Populationen und Artengemeinschaften kann Vorhersagen darüber ermöglichen wie Organismen in Zukunft auf sich ändernde Umweltbedingungen reagieren werden. Auf Merkmalen basierende Ansätze sind vielversprechend, da diese ebenso wie Umweltbedingungen verallgemeinbar und unabhängig vom Standort der entsprechenden Erhebung sein sollen. Erkenntnisse aus deren Beziehung wären dann skalenunabhängig und übertragbar auf andere Systeme. In der Theorie ermöglicht dies die Ableitung von generellen Trends sowie Vorhersagen für alle Ebenen biologischer Organisation, für andere geografische Regionen oder Vorhersagen in die Zukunft.

In dieser Arbeit untersuche ich wie sich ändernde Umweltfaktoren und Merkmale von Organismen sowie deren Interaktion die Struktur und die Dynamik von Artengemeinschaften auf unterschiedlichen räumlichen und zeitlichen Skalen beeinflussen. Um Vorhersagen ableiten zu können, wie ökologische Gemeinschaften in der Zukunft auf fortschreitende Umweltveränderungen reagieren werden, ist es notwendig zu verstehen wie (I) Artengemeinschaften allgemein auf sich natürlich ändernde Umweltbedingungen reagieren, (II) welche Merkmale für den Erfolg von Arten verantwortlich sind und (III) wie Merkmale den Erfolg einer Art in Abhängigkeit von gegebenen Umweltbedingungen beeinflussen.

In Kapitel 2 stelle ich drei Studien vor, die sich mit der Reaktion von Artengemeinschaften auf sich ändernde Umweltbedingungen entlang natürlicher Gradienten in terrestrischen Waldökosystemen beschäftigen. Die erste Studie untersucht die Auswirkungen der klimatischen Veränderung entlang eines lokalen Höhengradienten im Nationalpark Bayerischer Wald. Hier stelle ich den starken Effekt der Höhe über dem Meeresspiegel auf die Alpha-, Beta- und Gamma-Diversität von 15 Organismengruppen innerhalb der Pflanzen, Tiere und Pilze dar. Die Beta-Diversität zwischen den Höhenstufen trug hierbei den größten Anteil zur gesamten Gamma-Diversität in der Region bei. Die zweite Studie untersucht die Reaktion von Artengemeinschaften entlang des Verlaufs der Sukzession von Waldgesellschaften der gemäßigten Breiten mithilfe eines sogenannten ‚space-for-time substitution' Ansatzes. Die Ergebnisse zeigten, dass Veränderungen der Waldstrukturparameter entlang der Sukzession, von der frühen Etablierungsphase bis zur späteren Zerfallsphase, die Biodiversität im Wald stark beeinflussen. Frühe und späte Waldwachstumsphasen waren für die meisten Gruppen von größter Bedeutung. Gleichzeitig sind es diese Phasen, die in der konventionellen Forstwirtschaft eher unterrepräsentiert sind. Der Artenumsatz zwischen Flächen mit unterschiedlichen Waldwachstumsphasen trug dabei maßgeblich zum regionalen Artenpool bei. Dies unterstreicht die Bedeutung der Erhaltung von Waldlandschaften mit angemessener Repräsentierung aller Waldwachstumsphasen. In der dritten Studie untersuchte ich die Auswirkungen von sich ändernden klimatischen und waldstrukturellen Bedingungen in einem größeren räumlichen Maßstab, dem Verbreitungsgebiet der Rotbuche *Fagus sylvatica*. Hier untersuchte ich Artengemeinschaften von Arthropoden, die den Zunderschwamm *Fomes*

fomentarius bewohnen. Die Analyse der Artenzusammensetzung der 59 Standorte zielte darauf ab, die relative Bedeutung von Klima, Geographie und Waldstruktur für die Vorhersage der Alpha- und Beta-Diversität auf kontinentalem Maßstab zu quantifizieren. Interessanterweise waren die Arthropodengemeinschaften in Fruchtkörpern von *Fomes fomentarius* nur äußerst schwach von großräumigen Umweltgradienten geprägt. Für die Vielfalt in Konsolenpilzfruchtkörpern wie dem Zunderschwamm ist vor allem das lokale Vorkommen dieser Struktur von Bedeutung. Dies bestätigt Empfehlungen Bäume mit Pilzfruchtkörpern aus der Nutzung zu nehmen und als Habitatbäume zu schützen.

In Kapitel 3 stelle ich zwei Studien vor, die sich mit dem Erfolg von phytophagen Insektenarten beschäftigen. In beiden Studien wird der häufig beobachtete Zusammenhang von lokaler Verbreitung und mittlerer Dichte untersucht. In der ersten Studie wurde die dynamische Natur dieser Beziehung aufgezeigt wobei Hypothesen, deren Annahmen auf strukturellen Mechanismen basierten, falsifiziert werden konnten. Die Ergebnisse zeigten, dass bei phytophagen Insekten das dynamische Verhältnis von Verbreitung und Häufigkeit vor allem durch die Verfügbarkeit von qualitativ hochwertigem Habitat in der umgebenden Landschaft beeinflusst wird. Auf der untersuchten räumlichen Skala können Arten eine größere Verbreitung erreichen, wenn ausreichend Habitat in der Umgebung die Erfolgswahrscheinlichkeit von Ausbreitungsereignissen erhöht. Die erhöhte Rate erfolgreicher Ausbreitungsereignisse minimiert das Risiko eines lokalen Aussterbens der Population durch stochastische Prozesse und erhöht lokal die Populationsdichte. Ein wichtiger Aspekt dieser Studie war das Einbeziehen der Habitatqualität, die den stärksten Effekt auf die Verbreitung der Arten hatte. Dies wird in vergleichbaren Studien oft vernachlässigt. Die zweite Studie baute auf dem resultierenden, kausalen Pfadmodell der ersten Studie auf und erweiterte dieses. Hierbei zeigte sich, dass ökologisch vorteilhafte, morphologische Merkmale nur dann zu größerem Erfolg der Art führen, wenn erhöhte energetische Kosten durch eine gesteigerte Energieaufnahme oder effizientere Fortbewegung kompensiert werden. Die Studie veranschaulicht die Bedeutung des Energiebudgets von Organismen für deren Erfolg. Gleichzeitig wird das Potenzial der Integration dynamischer Energiebudgetmodelle in ökologische und populationsdynamische Fragestellungen unterstrichen. Diese Studie bestätigte außerdem den kausalen Rahmen, in dem die Habitatverfügbarkeit der wichtigste Treiber der lokalen Verbreitung von Arten und daraus resultierend deren lokaler Dichte ist.

In Kapitel 4 stelle ich zwei Studien vor, in denen die Kovarianz zwischen morphologischen Merkmalen einer Art und sie umgebende Umweltbedingungen untersucht werden. Hier konzentrieren sich beide Studien auf thermoregulatorisch relevante funktionelle Merkmale aufgrund sich ändernder thermaler Umweltbedingungen entlang geographischer Gradienten. In der ersten Studie wurde ein großräumiger Ansatz über ganz Westeuropa implementiert. In diesem wurde untersucht, ob die mittlere Helligkeit von Spannerartengemeinschaften (Lepidoptera: Geometridae) mit nach Norden abnehmender Solarstrahlung ebenso abnimmt. Hier wird davon ausgegangen, dass die Körperhelligkeit die Thermoregulation von Insekten beeinflusst. Tatsächlich zeigten die Ergebnisse, dass nördliche Spannerartengemeinschaften im Mittel dunkler sind als Gemeinschaften in Südeuropa. Im Allgemeinen stimmt dieses

Ergebnis mit vergleichbaren Studien zur Helligkeit von Insekten überein. In dieser Studie wurde dieses Muster zum ersten Mal auch bei nachtaktiven Insekten nachgewiesen. Die zweite Studie zeigte, dass die Beziehung von Farbhelligkeit und thermischer Umgebung bei nachtaktiven Spannern auf lokaler Ebene wiederum nicht nachweisbar ist. Hier hatte die Habitatverfügbarkeit eine größere Bedeutung. Die in dieser Studie ebenfalls untersuchten Schwärmer (Lepidoptera: Noctuidae) zeigten im Gegensatz dazu eine starke Beziehung zwischen den thermoregulatorischen Merkmalen Helligkeit und Körpergröße und der thermalen Umgebung. Größere und dunklere Arten waren in kühleren, höheren Lagen häufiger während kleine und helle Arten in den wärmeren, tieferen Lagen dominierten. Beide Studien deuten darauf hin, dass Beziehungen zwischen Artmerkmalen und Umweltbedingungen auf unterschiedlichen räumlichen Skalen und zwischen taxonomischen Gruppen stark variieren können. Dies steht im Widerspruch zu den Annahmen von auf Merkmalen basierenden Forschungsansätzen in der Ökologie und erschwert verlässliche Vorhersagen für die Zukunft.

Wir sind noch weit davon entfernt mithilfe von ökologischen Modellen zuverlässig vorherzusagen wie Individuen, Populationen oder ganze Artengemeinschaften auf Umweltveränderungen reagieren werden. Die Untersuchung relevanter Umweltgradienten, welche die Dynamik von Artengemeinschaften beeinflussen (Kapitel 2), die Bestimmung relevanter Artmerkmale, welche den Erfolg oder Misserfolg von Organismen bestimmen (Kapitel 3) sowie die Analyse der interaktiven Auswirkungen dieser Umweltbedingungen und Artmerkmale auf das Vorkommen von Arten (siehe Kapitel 4) wie sie in dieser Arbeit präsentiert wurden können uns helfen relevante Treiber für Arten und Artengemeinschaften in bestimmten raum-zeitlichen Kontexten zu identifizieren. Obwohl es derzeit nicht möglich erscheint, verlässliche und verallgemeinerbare Vorhersagen darüber zu generieren, wie sich Änderungen der makroklimatischen Bedingungen oder der Landnutzung auf die terrestrischen Gemeinschaften insgesamt auswirken werden, bieten die vorgestellten Ergebnisse wertvolle Erkenntnisse darüber, wie Organismen mit ihrer Umgebung interagieren. Genauso unvorhersehbar wie aktuell die Zukunft der uns umgebenden Umwelt erscheint, so unvorhersehbar wird auch die Antwort der Natur auf diese Veränderungen sein.

Chapter 7.1

Appendix chapter 2.2

Biodiversity along temperate forest succession

with
Torben Hilmers | Claus Bässler | Marco Heurich | Roland Brandl | Hans Pretzsch | Rupert Seidl | Jörg Müller |

published in Journal of Applied Ecology, 55 (6), 2018, p. 2756– 2766

Soil characteristics and macroclimate

Soil samples were collected as described in Peura *et al.* (2016). We explicitly considered information on soil pH, cation exchange capacity, base saturation and soil moisture, and performed a principal component analysis (PCA) based on the correlation matrix. In the subsequent analyses, we used the first principle component to control for differences in soil conditions. It explained 40% of the variance in the data and describes a gradient from dry, acidic, nutrient-poor soils to moist, alkaline and nutrient-rich soils. To correct for climatic differences between the observations, we used elevation as an additional covariate, as there is a strong linear relationship between important climatic variables and elevation in our study area (Fig. 7.1.1).

LiDAR single-tree detection

The bounding polygons of individual tree crowns were used to extract canopy variables and to distinguish deciduous from coniferous trees (Yao et al. 2012). Stem volume (m^3) and diameter at breast height (cm; DBH) of the extracted trees were determined using multiple linear regressions based on reference trees measured in the field (Heurich and Thoma 2008).

Taxonomic groups

Higher plants, fungi, and birds were recorded on all 287 plots for which forest structure was characterized. The other 20 taxonomic groups were sampled on subsets of the study plots due to labor-intensive collection methods. We used field collections (gastropods, number of study plots surveyed, n = 108; lichen and mosses, n = 109), flight-interception traps (beetles, true bugs, cicadas, bees and wasps, lacewings, spiders and harvestmen, n = 178), pitfall traps (beetles, true bugs, cicadas, springtails, spiders and harvestmen, mice and shrews, n = 178; gastropods, n = 108), malaise traps (cicadas, grasshoppers, lacewings, sawflies, hoverflies and other dipterans, n = 36), light traps (moths, n = 36), ultrasound recordings (bats, n = 29) and hand-sorted soil samples (worms, n = 87). For details of the sampling methods used for different taxa, see (Bässler et al. 2009). Note that some groups were sampled using several methods. To use the full spectrum of species for our analyses, we aggregated the data by summing the abundances across the consistent sampling methods across plots.

TABLE 7.1.1. The observed 23 taxonomic groups, their association with the 6 functional groups, and the number of plots (n) on which data were collected in the field.

Functional group	Taxon	n
Producer	Lichen	109
	Mosses	109
	Plants	287
Consumer I	Bees and wasps	36
	Beetles	178
	Cicadas	36
	Dipterans	36
	Grasshoppers	36
	Hoverflies	36
	Mice	178
	Moths	36
	Sawflies	36
	Snails	108
	True bugs	178
Consumer II	Beetles	178
	Dipterans	36
	Harvestmen	178
	Lacewings	36
	Snails	108
	Spiders	178
	True bugs	178
Consumer III	Bats	29
	Birds	286
	Shrews	178
Saprotroph	Beetles	178
	Dipterans	36
	Moths	36
	Snails	108
	Springtails	178
	Worms	87
Saproxylic organisms	Beetles	178
	Fungi	287
	Moths	36

TABLE 7.1.2. Results of the generalized linear mixed model with Poisson error and an observation-level random effect of the abundances (number of individuals recorded by all methods) for 33 functional groups. Predictor variables were the forest succession stages as an ordered factor with linear and quadratic contrasts, elevation and soil parameters of the plots.

	Taxon	Plots (n)	Species (n)	Forest succession stage				Elevation		Soil		R^2_C
				Linear		Quadratic						
Producer	Lichen	109	157	0.27	n.s.	**3.05**	**	**2.21**	*	0.61	n.s.	0.18
	Mosses	109	119	0.31	n.s.	**2.27**	*	−1.13	n.s.	0.05	n.s.	0.05
	Plants	287	181	0.59	n.s.	**6.85**	***	**7.29**	***	**4.64**	***	0.41
Consumer I	Bees and wasps	178	140	−0.56	n.s.	**8.39**	***	**4.95**	***	1.84	.	0.51
	Beetles	178	143	−1.18	n.s.	**2.83**	**	**5.04**	***	−1.01	n.s.	0.29
	Cicadas	36	97	−0.03	n.s.	**2.96**	**	**2.50**	*	0.70	n.s.	0.35
	Dipterans	36	6	−0.39	n.s.	0.00	n.s.	−0.48	n.s.	**2.62**	**	0.18
	Grasshoppers	36	11	0.00	n.s.	1.61	n.s.	−0.33	n.s.	−0.84	n.s.	0.10
	Hoverflies	36	113	−0.16	n.s.	**3.88**	***	0.93	n.s.	**2.21**	*	0.42
	Mice	178	4	−0.49	n.s.	0.83	n.s.	−0.18	n.s.	0.44	n.s.	0.02
	Moths	36	341	0.20	n.s.	0.26	n.s.	0.30	n.s.	0.05	n.s.	0.00
	Saw flies	36	103	−0.25	n.s.	1.87	.	1.92	.	**2.02**	*	0.27
	Snails	108	11	−1.07	n.s.	−0.80	n.s.	**−3.47**	***	**2.38**	*	0.23
	True bugs	178	50	−0.88	n.s.	**2.67**	**	**4.99**	***	0.67	n.s.	0.29
Consumer II	Beetles	178	365	0.12	n.s.	1.73	.	**3.08**	**	−1.23	n.s.	0.13
	Dipterans	36	30	0.03	n.s.	−0.80	n.s.	**−3.41**	***	−1.11	n.s.	0.30
	Harvestmen	178	9	−0.03	n.s.	**−2.46**	*	**2.69**	**	−0.53	n.s.	0.07
	Lacewings	36	27	−0.56	n.s.	0.84	n.s.	**2.60**	**	**2.17**	*	0.28
	Snails	108	7	1.85	.	1.83	.	**5.00**	***	**2.44**	*	0.32
	Spiders	178	143	−0.64	n.s.	1.60	n.s.	1.12	n.s.	0.15	n.s.	0.04
	True bugs	178	43	0.32	n.s.	−0.54	n.s.	**4.42**	***	−1.01	n.s.	0.15
Consumer III	Bats	29	14	−0.87	n.s.	0.31	n.s.	−0.14	n.s.	0.67	n.s.	0.05
	Birds	286	70	1.62	n.s.	1.03	n.s.	**−3.31**	***	**2.33**	*	0.10
	Shrews	178	3	−0.10	n.s.	1.52	n.s.	−0.22	n.s.	−0.62	n.s.	0.02
Saprotroph	Beetles	178	38	−0.09	n.s.	**3.47**	***	**−2.87**	**	−1.28	n.s.	0.08
	Dipterans	36	20	0.90	n.s.	0.20	n.s.	−0.31	n.s.	0.02	n.s.	0.04
	Moths	36	14	0.79	n.s.	0.56	n.s.	**−3.60**	***	0.52	n.s.	0.42
	Snails	108	24	1.68	.	0.88	n.s.	**−5.62**	***	−0.03	n.s.	0.36
	Springtails	178	40	−1.17	n.s.	1.71	.	−1.08	n.s.	−0.13	n.s.	0.02
	Worms	87	8	**2.24**	*	0.01	n.s.	−1.80	.	**3.04**	**	0.25
Saproxylic organism	Beetles	178	237	**−3.13**	**	**5.75**	***	−0.54	n.s.	0.52	n.s.	0.23
	Fungi	287	269	**2.83**	**	−0.02	n.s.	−1.54	n.s.	−1.72	.	0.06
	Moths	36	16	−0.80	n.s.	0.34	n.s.	**−4.28**	***	1.50	n.s.	0.45

Notes. Given are the numbers of plots, overall species numbers, z-values of the predictors and the conditional R^2 of the model (Nakagawa and Schielzeth 2013). Significant effects are given in bold. Significant codes: n.s., not significant; ., 0.1; *, 0.05; **, 0.01; ***, <0.001.

TABLE 7.1.3. Results of the generalized linear mixed model with Poisson error and an observation-level random effect of the number of species (recorded by all methods) for 33 functional groups. Predictor variables were the forest succession stages as an ordered factor with linear and quadratic contrasts, elevation and soil parameters of the plots.

	Taxon	Plots (n)	Spe-cies (n)	Forest succession stage				Elevation		Soil		R^2_C
				Linear		Quadratic						
Producer	Lichen	109	157	1.07	n.s.	**3.10**	**	**2.60**	**	0.99	n.s.	0.19
	Mosses	109	119	0.13	n.s.	**2.61**	**	−1.50	n.s.	1.17	n.s.	0.08
	Plants	287	181	**2.98**	**	1.83	.	**2.65**	**	**7.59**	***	0.21
Consumer I	Bees and wasps	178	140	−0.92	n.s.	**7.85**	***	**4.82**	***	1.72	.	0.48
	Beetles	178	143	0.83	n.s.	**4.63**	***	**2.99**	**	**1.99**	*	0.22
	Cicadas	36	97	−0.43	n.s.	**4.06**	***	0.43	n.s.	1.12	n.s.	0.38
	Dipterans	36	6	−1.07	n.s.	0.45	n.s.	−0.65	n.s.	1.46	n.s.	0.13
	Grasshoppers	36	11	0.49	n.s.	**2.48**	*	−0.93	n.s.	−1.25	n.s.	0.24
	Hoverflies	36	113	0.57	n.s.	**3.72**	***	1.06	n.s.	**2.48**	*	0.42
	Mice	178	4	−0.74	n.s.	1.36	n.s.	−0.26	n.s.	0.77	n.s.	0.09
	Moths	36	341	0.17	n.s.	0	n.s.	−0.20	n.s.	0.77	n.s.	0.03
	Saw flies	36	103	0.32	n.s.	1.49	n.s.	**2.63**	**	1.92	.	0.28
	Snails	108	11	−0.22	n.s.	−0.71	n.s.	**−3.09**	**	**3.72**	***	0.27
	True bugs	178	50	−1.53	n.s.	**3.65**	***	**3.98**	***	1.24	n.s.	0.29
Consumer II	Beetles	178	365	0.20	n.s.	1.45	n.s.	−0.28	n.s.	0.51	n.s.	0.01
	Dipterans	36	30	1.26	n.s.	1.38	n.s.	**−3.30**	***	−0.71	n.s.	0.33
	Harvestmen	178	9	0.37	n.s.	−1.55	n.s.	0.82	n.s.	−0.01	n.s.	0.02
	Lacewings	36	27	−1.48	n.s.	0.34	n.s.	1.31	n.s.	**2.67**	**	0.25
	Snails	108	7	1.42	n.s.	0.88	n.s.	1.32	n.s.	**4.09**	***	0.15
	Spiders	178	143	−1.39	n.s.	**3.87**	***	0.89	n.s.	**2.18**	*	0.15
	True bugs	178	43	0.31	n.s.	−0.34	n.s.	**4.04**	***	0.25	n.s.	0.13
Consumer III	Bats	29	14	−1.65	.	1.37	n.s.	−0.26	n.s.	1.24	n.s.	0.23
	Birds	286	70	0.29	n.s.	**2.99**	**	**−4.81**	***	**2.24**	*	0.13
	Shrews	178	3	0.48	n.s.	1.01	n.s.	−0.43	n.s.	−0.28	n.s.	0.01
Saprotroph	Beetles	178	38	0.80	n.s.	0.85	n.s.	−0.59	n.s.	−1.07	n.s.	0.01
	Dipterans	36	20	1.13	n.s.	0.16	n.s.	−1.21	n.s.	0.30	n.s.	0.13
	Moths	36	14	1.67	.	−1.14	n.s.	**−3.54**	***	1.09	n.s.	0.49
	Snails	108	24	0.88	n.s.	1.36	n.s.	**−4.02**	***	**3.73**	***	0.31
	Springtails	178	40	0.13	n.s.	1.06	n.s.	−1.84	.	−1.32	n.s.	0.03
	Worms	87	8	1.61	n.s.	−0.25	n.s.	−1.95	.	**2.4**	*	0.24
Saproxylic organism	Beetles	178	237	−0.78	n.s.	**4.46**	***	−1.52	n.s.	1.65	.	0.12
	Fungi	287	269	**3.80**	***	**−4.39**	***	**−6.60**	***	0.29	n.s.	0.38
	Moths	36	16	0.50	n.s.	1.42	n.s.	**−4.07**	***	0.89	n.s.	0.44

Notes. Given are the numbers of plots, overall species numbers, z-values of the predictors and the conditional R^2 of the model (Nakagawa and Schielzeth 2013). Significant effects are given in bold. Significant codes: n.s., not significant; ., 0.1; *, 0.05; **, 0.01; ***, <0.001.

TABLE 7.1.4. Results of the generalized linear mixed model with Poisson error and an observation-level random effect of the number of species (recorded by all methods) for 33 functional groups. Predictor variables were the forest succession stages as an ordered factor with linear and quadratic contrasts, elevation, soil parameters of the plots, and abundance of the species.

	Taxon	Plots (n)	Species (n)	Forest successional stage: Linear		Forest successional stage: Quadratic		Elevation		Soil		Abundance		R^2_C
Producer	Lichens	109	157	1.21	n.s.	0.50	n.s.	0.20	n.s.	1.00	n.s.	**16.30**	***	0.78
	Mosses	109	119	0.22	n.s.	0.64	n.s.	−1.41	n.s.	**2.58**	**	**18.50**	***	0.73
	Plants	287	181	**3.82**	***	−1.37	n.s.	−0.46	n.s.	**6.07**	***	**7.39**	***	0.43
Consumer I	Bees and wasps	178	140	0.48	n.s.	1.40	n.s.	**2.68**	**	0.11	n.s.	**11.60**	***	0.68
	Beetles	178	143	**2.66**	**	**2.95**	**	0.35	n.s.	**2.86**	**	**8.17**	***	0.41
	Cicadas	36	97	−0.38	n.s.	**2.47**	*	−0.91	n.s.	1.44	n.s.	**9.30**	***	0.73
	Dipterans	36	6	−1.23	n.s.	0.31	n.s.	−0.78	n.s.	−0.25	n.s.	**3.31**	***	0.38
	Grasshoppers	36	11	−0.82	n.s.	0.89	n.s.	0.43	n.s.	−1.05	n.s.	**4.46**	***	0.52
	Hoverflies	36	113	0.57	n.s.	0.25	n.s.	0.47	n.s.	0.73	n.s.	**9.57**	***	0.83
	Mice	178	4	0.74	n.s.	0.21	n.s.	0.60	n.s.	0.38	n.s.	**5.33**	***	0.25
	Moths	36	341	0.69	n.s.	−0.67	n.s.	−1.29	n.s.	0.47	n.s.	**12.5**	***	0.82
	Saw flies	36	103	0.11	n.s.	−1.21	n.s.	**3.40**	***	0.61	n.s.	**9.60**	***	0.79
	Snails	108	11	−0.02	n.s.	0.04	n.s.	−0.65	n.s.	1.05	n.s.	**6.35**	***	0.42
	True bugs	178	50	−1.51	n.s.	**4.76**	***	1.09	n.s.	**2.06**	*	**7.75**	***	0.46
Consumer II	Beetles	178	365	0.20	n.s.	0.39	n.s.	**−3.27**	**	**2.02**	*	**12.90**	***	0.49
	Dipterans	36	30	1.17	n.s.	**2.33**	*	−1.68	.	0.18	n.s.	**3.78**	***	0.49
	Harvestmen	178	9	0.14	n.s.	−0.25	n.s.	−0.96	n.s.	0.75	n.s.	**9.02**	***	0.31
	Lacewings	36	27	−0.74	n.s.	0.19	n.s.	−0.96	n.s.	0.77	n.s.	**4.60**	***	0.50
	Snails	108	7	0.79	n.s.	0.38	n.s.	−0.48	n.s.	**2.56**	*	**4.35**	***	0.27
	Spiders	178	143	−0.49	n.s.	**3.00**	**	−0.28	n.s.	**2.37**	*	**10.10**	***	0.45
	True bugs	178	43	0.05	n.s.	−0.05	n.s.	1.76	.	1.13	n.s.	**8.06**	***	0.33
Consumer III	Bats	29	14	−1.43	n.s.	1.28	n.s.	−0.18	n.s.	1.23	n.s.	1.76	.	0.28
	Birds	286	70	−0.26	n.s.	1.45	n.s.	**−2.04**	*	0.57	n.s.	**12.70**	***	0.43
	Shrews	178	3	0.48	n.s.	0.04	n.s.	−0.42	n.s.	0.25	n.s.	**8.31**	***	0.37
Saprotroph	Beetles	178	38	1.47	n.s.	**−2.07**	*	**3.00**	**	−0.98	n.s.	**11.50**	***	0.38
	Dipterans	36	20	0.61	n.s.	0.29	n.s.	−1.50	n.s.	0.25	n.s.	**4.27**	***	0.33
	Moths	36	14	1.15	n.s.	−0.86	n.s.	−1.09	n.s.	−0.78	n.s.	**3.88**	***	0.48
	Snails	108	24	0.25	n.s.	1.18	n.s.	**−2.21**	*	**3.83**	***	**4.14**	***	0.38
	Springtails	178	40	0.52	n.s.	0	n.s.	−1.58	n.s.	−0.86	n.s.	**7.28**	***	0.25
	Worms	87	8	−0.21	n.s.	−0.17	n.s.	−0.93	n.s.	−0.84	n.s.	**6.44**	***	0.45
Saproxylic organism	Beetles	178	237	**2.48**	*	0.28	n.s.	−1.07	n.s.	1.68	.	**11.30**	***	0.49
	Fungi	287	269	**2.09**	*	**−4.45**	***	**−5.76**	***	1.54	n.s.	**10.10**	***	0.50
	Moths	36	16	0.53	n.s.	0.86	n.s.	−1.57	n.s.	−0.81	n.s.	**3.45**	***	0.49

Notes. Given are the numbers of plots, overall species numbers, z-values of the predictors and the conditional R^2 of the model (Nakagawa and Schielzeth 2013). Significant effects are given in bold. Significant codes: n.s., not significant; ., 0.1; *, 0.05; **, 0.01; ***, <0.001.

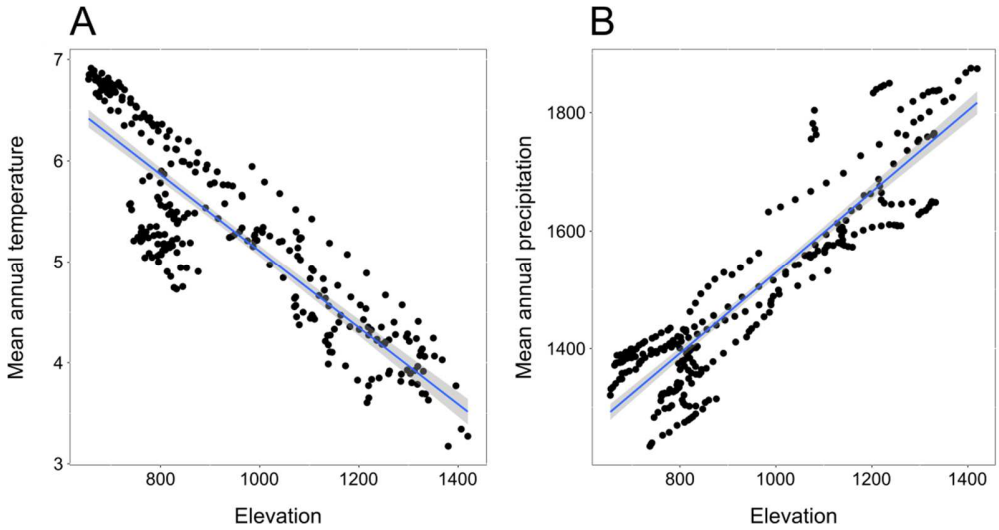

FIGURE 7.1.1. Climate of the study region based on interpolated data from 1980 to 2006. (A) Mean annual temperature (°C) in relation to elevation (m a.s.l.) of all 287 study plots. The blue regression line is based on a linear model; the grey area depicts the 95% confidence interval ($R^2 = 0.77$, $F_{1,285} = 937.6$, $P < 0.001$). (B) Mean annual precipitation (mm) in relation to elevation (m a.s.l.) of all 287 study plots. The blue regression line is based on a linear model, with the grey area depicting the 95% confidence interval ($R^2 = 0.82$, $F_{1,285} = 1299$, $P < 0.001$).

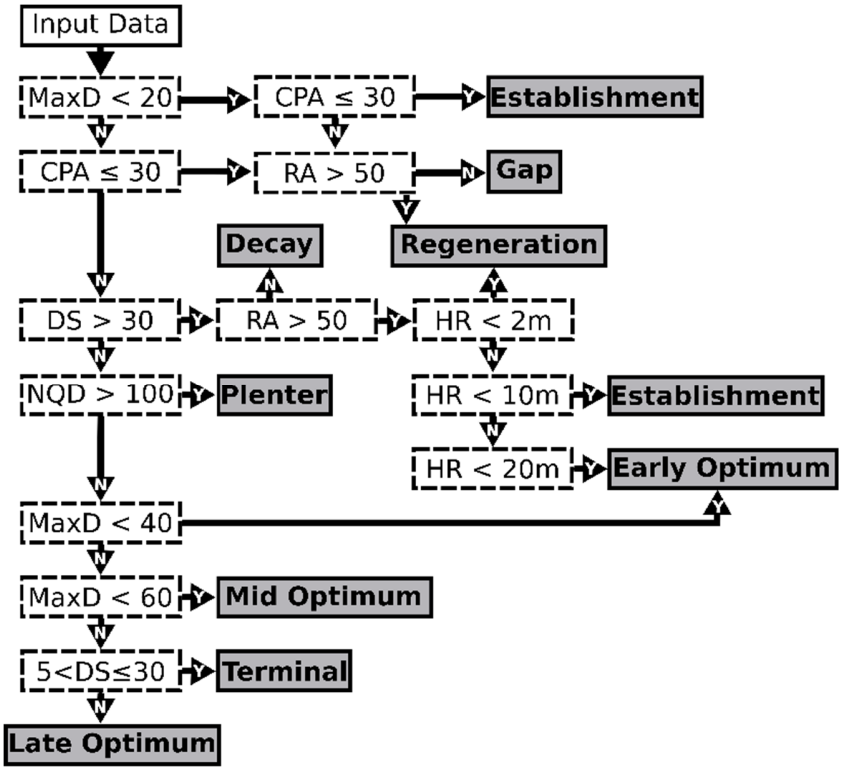

FIGURE 7.1.2. Decision tree for assigning forest succession stages using a modified classification protocol adapted from Tabaku (2000) and Zenner et al. (2016). Each primary attribute is evaluated as a dichotomy, which assigns 1000 m² circular plots differentially if the criterion is met (Y) or not met (N). CPA, canopy projection area [%]; maxD, maximum diameter at breast height (DBH) [cm]; DS, proportion of dead wood [%]; RA, regeneration area [%]; HR, regeneration height [m]; MeanD, mean DBH [cm]; NQD, normalized quartile of DBH.

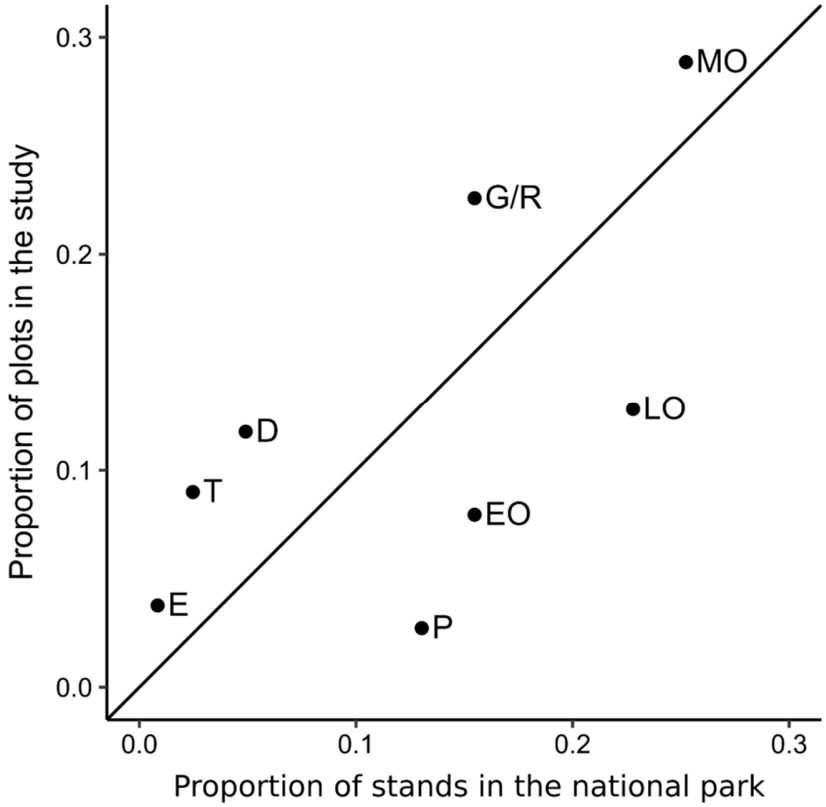

FIGURE 7.1.3. Comparison of the proportion of stages of forest succession in our study with the proportion in the surrounding Bavarian Forest National Park. Spearman rank correlation $\varrho = 0.67$; $P < 0.05$. Data for the national park is based on 123 plots of a forest inventory evenly distributed over the area of the park in the year 2013. Stages: G, gap; R, regeneration; E, establishment; EO, early optimum; MO, mid optimum; LO, late optimum; P, plenter; T, terminal; D, decay. As there was no explicit recording of trees with a diameter at breast height <7 cm in the inventory, we combined the gap and regeneration stages as described in Zenner et al. (2016).

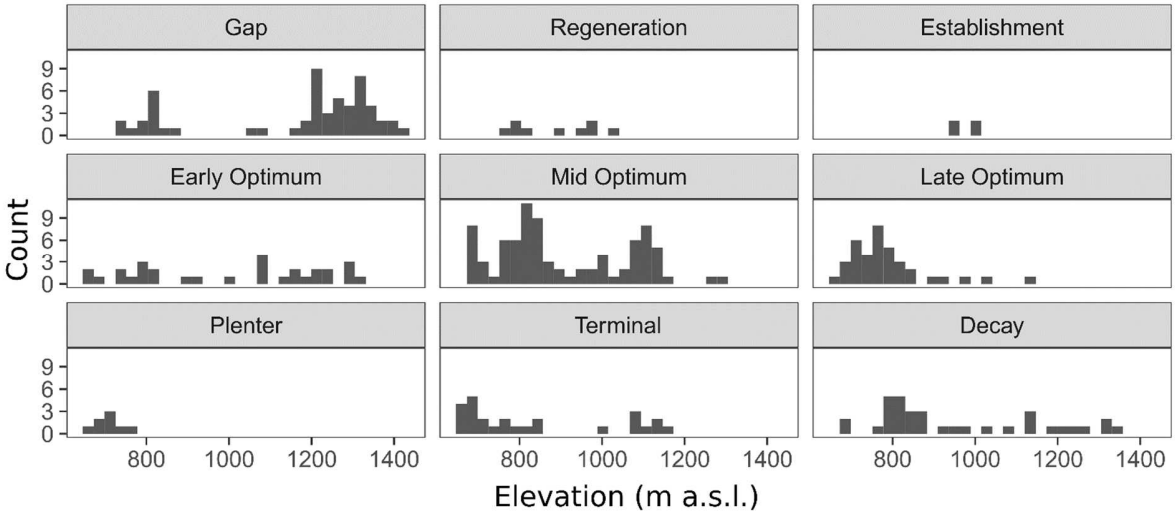

FIGURE 7.1.4. Histogram of the 287 plots and their forest succession stage across elevation.

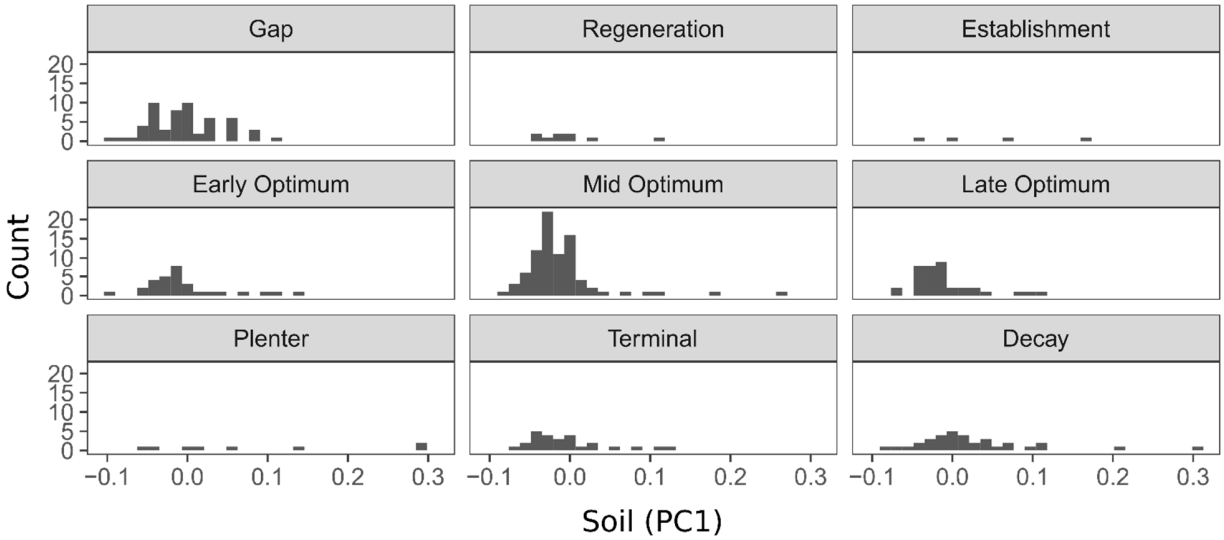

FIGURE 7.1.5. Histogram of the 287 plots and their forest succession stage across the first principal component of the PCA (PC1) on the soil variables, with low values indicating dry, acidic, nutrient-poor soils and high values indicating moist, alkaline and nutrient-rich soils.

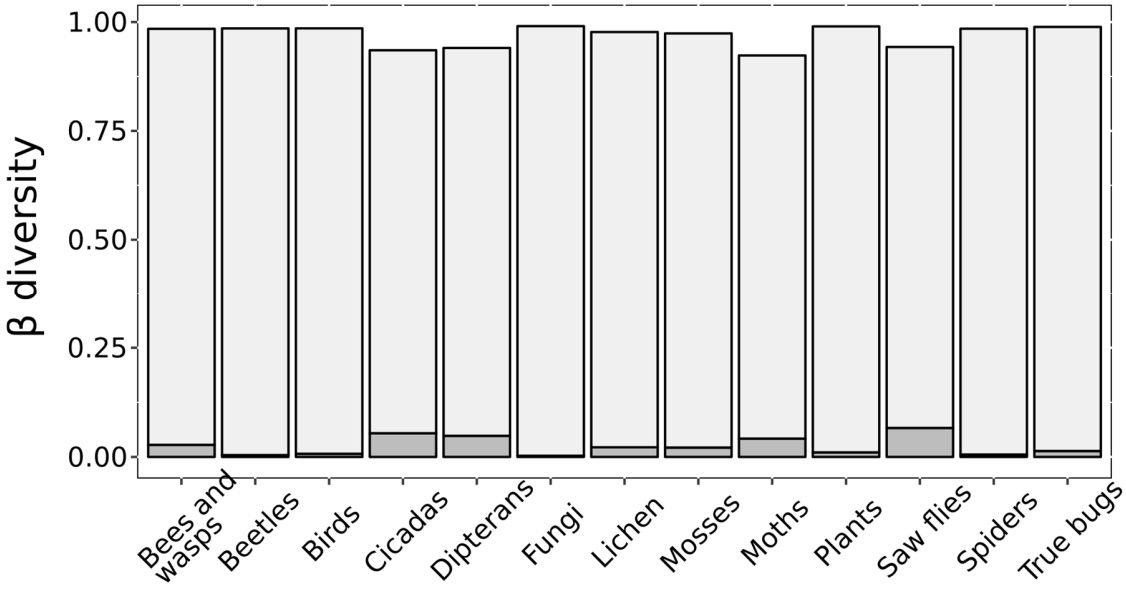

FIGURE 7.1.6. Multiple-site Sørensen dissimilarity of the taxa incorporated in the species composition analysis (i.e. excluding taxonomic groups with ≤ 30 species). The overall β-diversity was decomposed in its additive components turnover (light grey) and nestedness (dark grey).

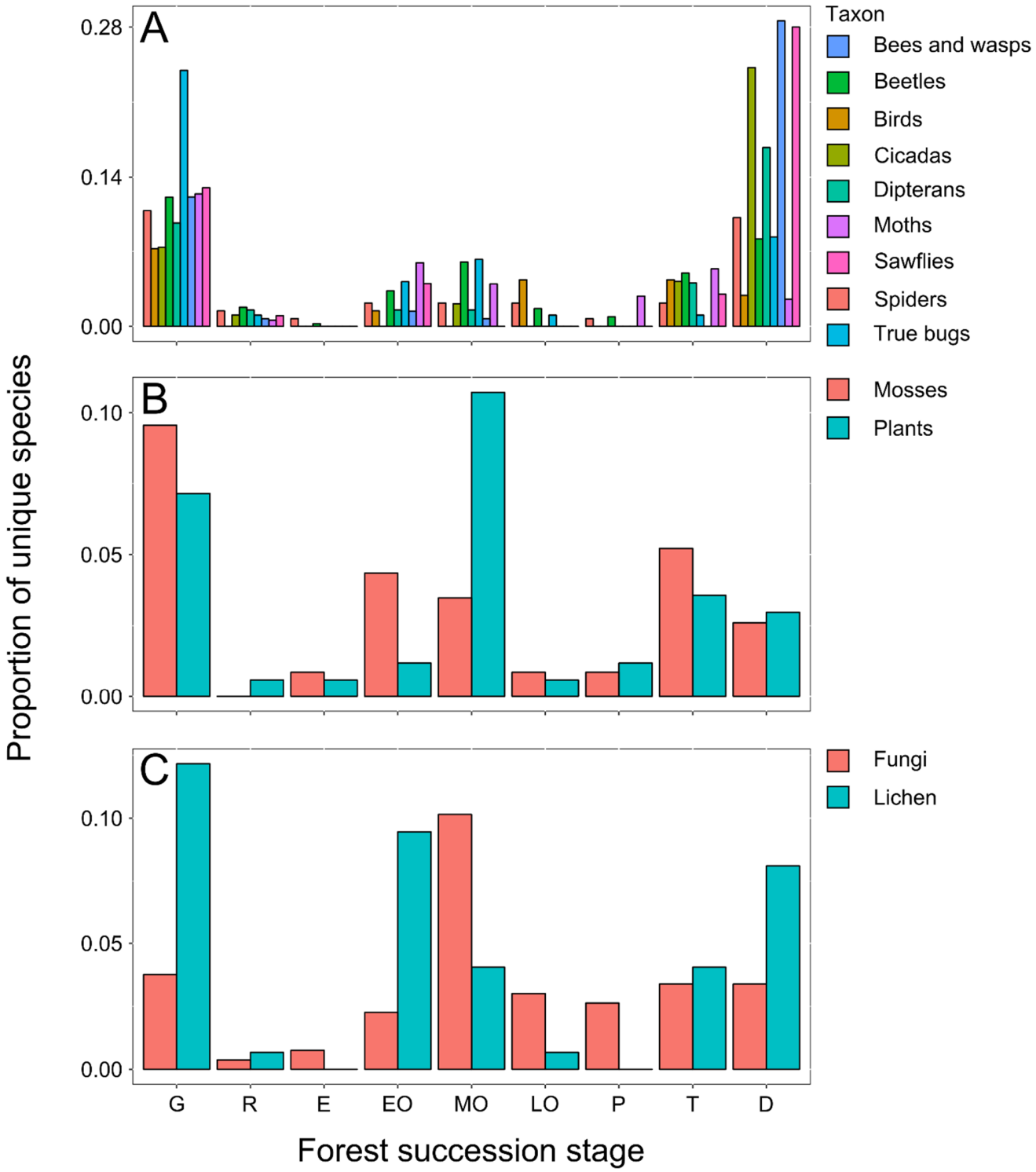

FIGURE 7.1.7. Number of species uniquely found in single stages of forest succession divided by the overall number of species observed for each taxon belonging to the kingdoms (A) animals, (B) plants and (C) fungi. Calculations were done for all taxa included in the species composition analyses (i.e. excluding taxonomic groups with ≤ 30 species). Stages: G, gap; R, regeneration; E, establishment; EO, early optimum; MO, mid optimum; LO, late optimum; P, plenter; T, terminal; D, decay.

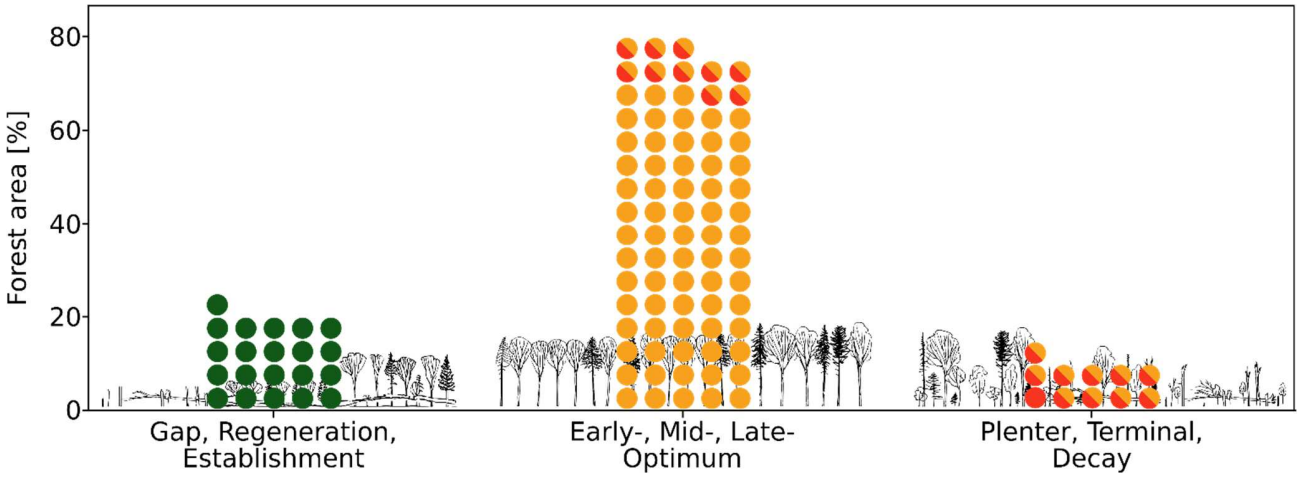

FIGURE 7.1.8- Distribution of the German forest area across forest succession stages. Data are from the second German national forest inventory (Thünen-Institut 2012). One circle represents 1% of the forest-covered area in Germany. For circles with two colors, an exact assignment to one of the two groups of forest succession stage was not possible.

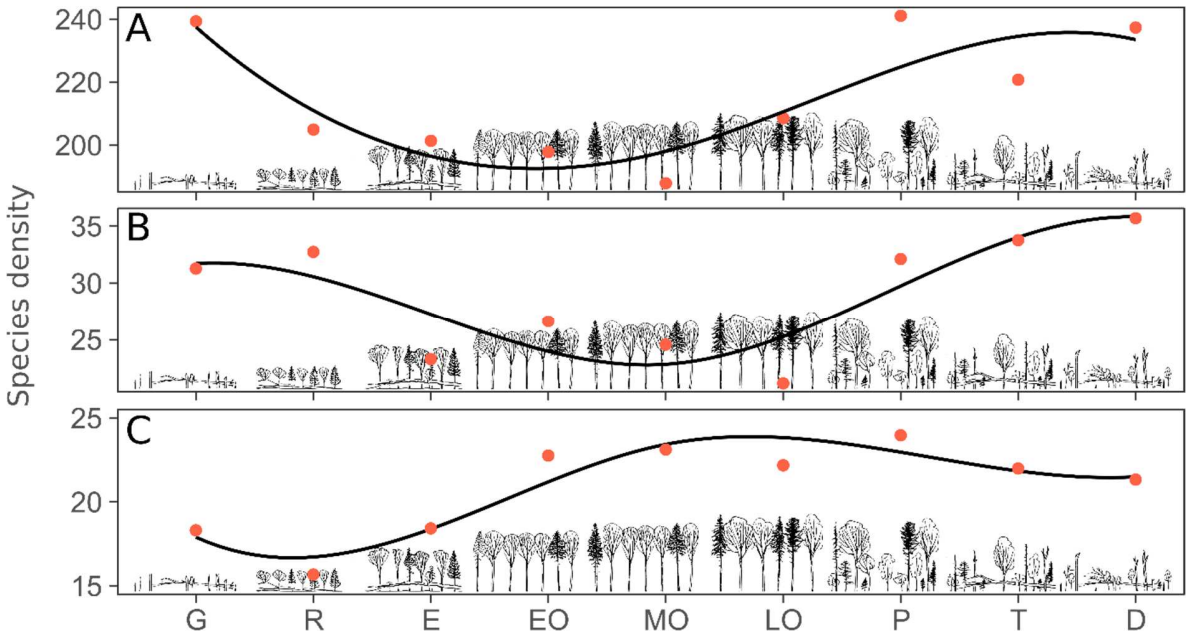

FIGURE 7.1.9. Variation in species density of the three kingdoms (A) animal (number of plots n = 36), (B) plants, (n = 114) and (C) fungi (n = 114) along stages of forest succession. Species density was predicted by summing up all predicted species densities for each taxon and each succession stage and assigning them to one of the three kingdoms. For the calculations, all taxa predictions are based on the plots shared by the taxa within, hence the low number of plots for animals. Lines were generated by fitting a loess curve. See Fig. 3 for the normalized sum of species densities in all three kingdoms. Stages: R, regeneration; E, establishment; EO, early optimum; MO, mid optimum; LO, late optimum; P, plenter; T, terminal; D, decay.

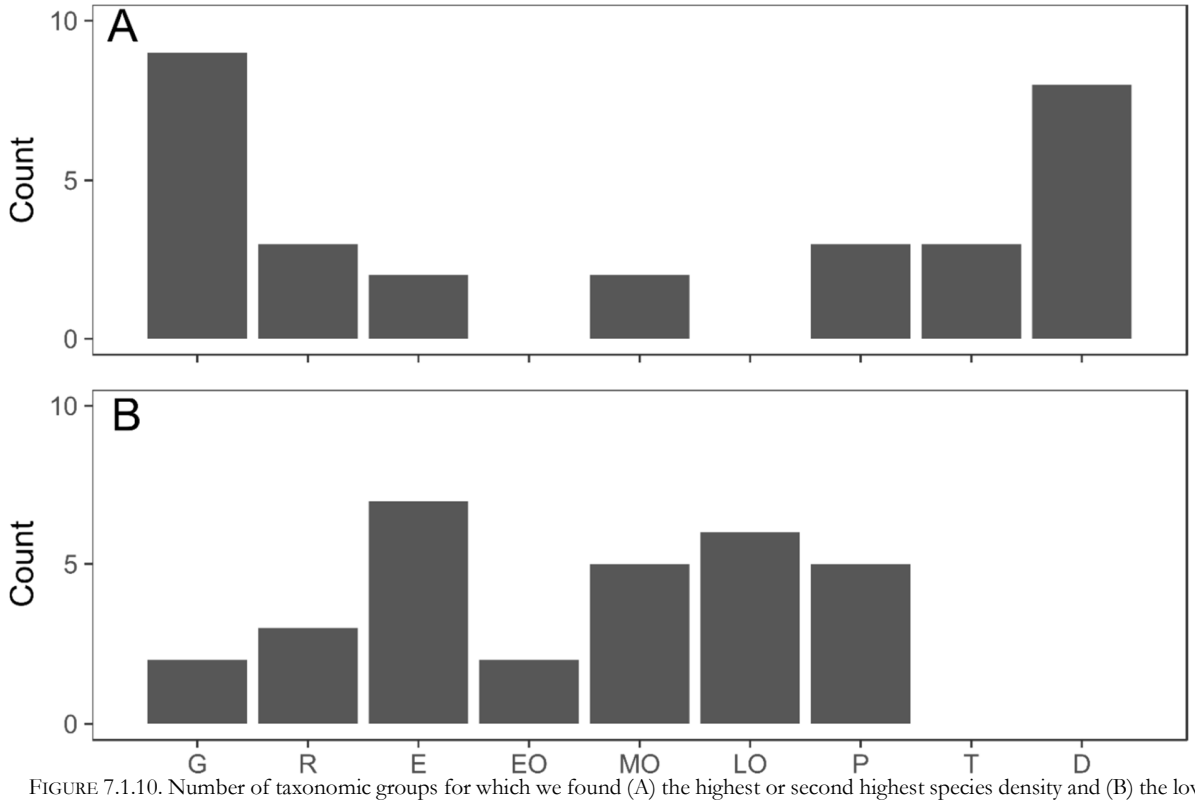

FIGURE 7.1.10. Number of taxonomic groups for which we found (A) the highest or second highest species density and (B) the lowest or second lowest species density in each forest succession stage. Only taxonomic groups with a significant response in species density to forest succession were considered. Stages: G, gap; R, regeneration; E, establishment; EO, early optimum; MO, mid optimum; LO, late optimum; P, plenter; T, terminal; D, decay.

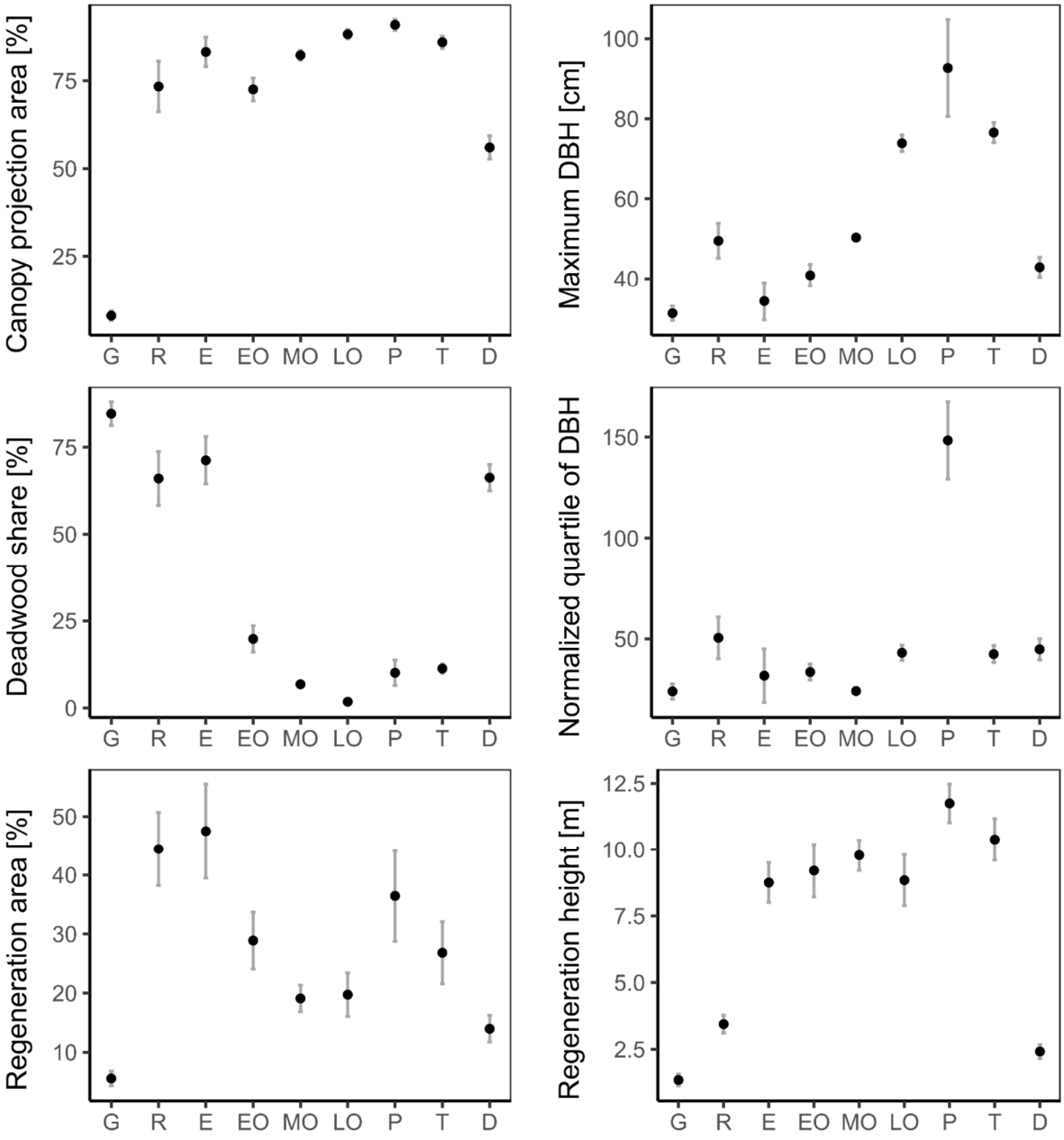

FIGURE 7.1.11. Characterization of the stages of forest succession with regards to the variables included in the decision tree. Values represent mean and standard error. Stages: G, gap; R, regeneration; E, establishment; EO, early optimum; MO, mid optimum; LO, late optimum; P, plenter; T, terminal; D, decay.

Chapter 7.2

Appendix chapter 2.3

Arthropod communities in fungal fruitbodies are weakly structured by climate and biogeography across European beech forests

with

Jörg Müller | Pablo Aramendi | Claus Bässler | Martin Brändle | Christophe Bouget | Antoine Brin | Heinz Bussler | Kostadin B. Georgiev | Radosław Gil | Martin M. Gossner | Jacob Heilmann-Clausen | Gunnar Isacsson | Anton Krištín | Thibault Lachat | Laurent Larrieu | Elodie Magnanou | Alexander Maringer | Ulrich Mergner | Martin Mikoláš | Lars Opgenoorth | Jürgen Schmidl | Miroslav Svoboda | Simon Thorn | Kris Vandekerkhove | Al Vrezec | Thomas Wagner | Maria-Barbara Winter | Livia Zapponi | Roland Brandl | Sebastian Seibold |

published in Diversity and Distributions, Early View: https://doi.org/10.1111/ddi.12882

Genetic analysis of Fomes fomentarius fruiting bodies

Methods

DNA-extraction of the *Fomes fomentarius*-fruitbodies was carried out by applying the fast microwave-based method proposed by Dörnte & Kües (2013). Sequences for the internal transcribed spacer (ITS) region and the elongation factor α (efa) gene were amplified by touchdown PCR. The ITS region was chosen because of its great interspecific discriminatory power (Martin & Rygiewicz 2005), whilst the efa gene appears to provide greater intraspecific variation which is needed for successfully discriminating different geographic lineages of *F. fomentarius* (Pristas et al. 2013). Alignments were carried out using the MUSCLE algorithm implemented in MEGA (version 5.1; Tamura et al. 2011).

Results

DNA extraction, amplification and sequencing were successful for samples from 36 sites for the ITS region (734 bp) and 14 sites for the efa gene (483 bp; see Figure 7.2.1). With the sequence data we were able to discriminate two genotypes of *F. fomentarius* as previously reported as sympatric cryptic species by Judova et al. (2012) for the ITS region and confirmed by Pristas et al. (2013) for efa in Eastern Slovakia. For the ITS region we found 16 variable nucleotide positions comprised of 14 heterozygous positions and two indels. Most of the variation was accounted for by the two genotypes, with 31 samples belonging to genotype A and five samples to genotype B (Table 7.2.1, Figure 7.2.1). The remaining eight variable nucleotides occurred on samples from six different sites. For the efa region we found 38 variable nucleotide positions and one indel, however, only one sample from Belgium and one from Ukraine showed genetic variation, all 12 others shared the same nucleotide sequences (Table 7.2.2).

Metabarcoding of arthropods inhabiting fruiting bodies

The non-beetle arthropod fauna was identified by metabarcoding using next generation sequencing carried out by AIM – Advanced Identification Methods GmbH (Munich, Germany). Therefore, all bulk samples were homogenized and DNA extracted using standardized protocols (DNEay Tissue Kit, Qiagen, Hilden, Germany). For PCR amplification of each individual sample, a unique 8 basepair barcoding tag was inserted into the mini-barcode primers of (Leray & Knowlton 2015; mlCOIintF 5' - GGW ACW GGW TGAACW GTW TAY CCY CC– 3', dgHco 5' - TAA ACT TCA GGG TGACCA AAR AAY CA– 3') targeting the mitochondrial CO1-5P region. Amplification success and DNA concentrations were checked via gel electrophoresis. For amplicon-pooling of parallel samples, approximately 20 ng of successfully amplified PCR products were used. A preparative gel electrophoresis was used for size-selection of the Illumina libraries, which were then subsequently sequenced on an Illumina MiSeq.

For processing of sequence data, we primarily used the OTU clustering-pipeline of USEARCH (Edgar 2010). Forward and reverse reads were first combined with the program -fastq_mergepairs, using default settings. Tags and primers were removed with cutadapt (Martin 2011), again using default settings. Sequences were then quality filtered with USEARCH -fastq_filter at maximum expected error = 1. Sequences outside of the 310-315 bp range were discarded. Pooled sequences were dereplicated (i.e. combining identical

sequencing reads), taking both strands into account, and discarding singletons. The dereplicated sequences were then clustered into Operational Taxonomic Units (OTUs) of 97% identity with -cluster_otus, a program which includes chimera removal. All of the originally merged sequences were matched against the OTUs to create an OTU table, using -usearch_global. The obtained OTUs were used within a CUSTOMBLAST command search in Geneious (v9.1.7 - Biomatters, Auckland - New Zealand) against a custom database created from the DNA barcode library of the publicly available Central European insect sequences within the Barcode of Life (BOLD – v4.boldsystems.org; for details see Morinière et al. 2016). Within BOLD, similar CO1 barcode sequences are assigned a globally unique identifier (Barcode Index Number - BIN; Ratnasingham & Hebert 2013). In order to account for sequencing errors and within-species variations, only BLAST hits of >97% similarity were included. From these matches, species lists (BIN lists) were constructed for sub- and mixed samples. When the best hit showed a similarity lower than 97%, the best genus-level or family-level hit was identified and used as operational taxonomic unit (OTU) but for simplicity, we refer to these as `species´. Species-sample matrices for beetles and all other arthropods were combined.

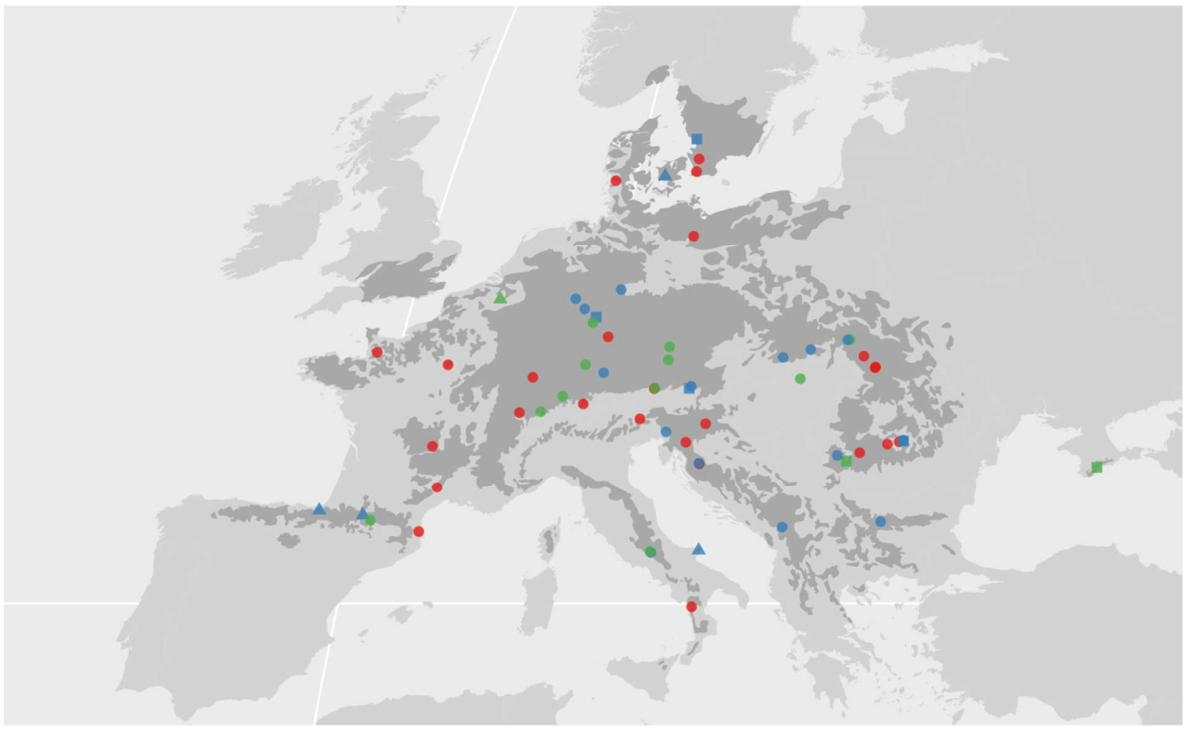

FIGURE 7.2.1. Study sites with indication for data availability. Green symbols indicate that genetic data based on both gene regions is available. Blue symbols indicate that the genetic information is only based on the ITS region. Red symbols indicate that no genetic data is available. The shape of the symbol indicates the genetic constitution of the *Fomes fomentarius* sample from the site. Circles represent genotype A, while triangles represent genotype B (in accordance with Judova et al. 2012). Squares indicate that variability was found on single nucleotide positions.

TABLE 7.2.1. Alignment of Fomes fomentarius internal transcribed spacer (ITS) sequences. Overall, we found 16 variable positions comprised of two indels and 14 additional heterozygous positions. Sequences with the seven nucleotide insertion are termed genotype B, whilst the other is termed genotype A in accordance with Judova et al. (2012). Variable positions are grey shaded.

	136 nt	23 nt	13 nt	254 nt	12 nt	16 nt	10 nt	20 nt	32 nt	8 nt	34 nt	119 nt
A Ges01	C A C	G - - T	C C T C G	A C C T T	G C G T T G G A T G T	C C C - - - - - - - - A G	T T A A	G T G	C A C C	G A T	T A T	
A_Ges02	C A C	G - - T	C C T C G	A C C T T	G G G T T G G A T G T	C C C - - - - - - - - A G	T T A A	G T G	C A C C	G A T	T T T	
AL_Ver	C A C	G - - T	C C T C G	A C C T T	G C G T T G G A T G T	C C C - - - - - - - - A G	T T A A	G T G	C A C C	G A T	T T T	
B_Son	C A C	G G A T	C T T T G	A C T T T	G G G T T G G C T A T	C C C T C G T T T G A G	T C A A	G C G	C G A C	G T T	T T T	
BUL_Boa	C A C	G - - T	C C T C G	A C C T T	G C G T T G G A T G T	C C C - - - - - - - - A G	T T A A	G T G	C A C C	G A T	T T T	
CH_Aug	C A C	G - - T	C C T C G	A C C T T	G C G T T G G A T G T	C C C - - - - - - - - A G	T T A A	G T G	C A C C	G W T	T T T	
CH_Sih	C A C	G - - T	C C T C G	A C C T T	G C G T T G G A T G T	C C C - - - - - - - - A G	T T G A	G T G	C A C C	G A T	T T T	
D_Aew08	C A C	G - - T	C C T C R	A C C T T	G C G T T G G A T G T	C C C - - - - - - - - A G	T T A A	G T G	C A C C	G A T	T T T	
D_Bgl2	C A C	G - - T	C C T C G	A C C T T	G C G T T G G A T G T	C C C - - - - - - - - A G	T T A A	G T G	C A C C	G A T	T T T	
D_Bw1	C A C	G - - T	C C T C G	A C C T T	G C G T T G G A T G T	C C C - - - - - - - - A G	T T A A	G T G	C A C C	G A T	T T T	
D_Bw2	C A C	G - - T	C C T C G	A C C T T	G C G T T G G A T G T	C C C - - - - - - - - A G	T T A A	G T G	C A C C	G A T	T T T	
D_Hew12			C C T C G	A C C T T	G C G T T G G A T G T	C C C - - - - - - - - A G	T T A A	G T G	C A C C	G A T	T T T	
D_Kem	C G C	G - - T	C C T C G	A C C T T	G C G T T G G A T G T	C C C - - - - - - - - A G	T T A A	G T G	C A C C	G A T	T T T	
D_Onw	C A C	G - - T	C C T C G	A C C T T	G C G T T G G A T G T	C C C - - - - - - - - A G	T T A A	G T G	C A C C	G A T	T T T	
D_Soed	C A C	G - - T	C C T C G	A C C T T	G C G T T G G A T G T	C C C - - - - - - - - A G	T T A A	G T G	C A C C	G A T	T T T	
D_Spe	C A C	G - - T	C C T C G	A C C T T	G C G T T G G A T G T	C C C - - - - - - - - A G	T T A A	G T G	C A C C	G A T	T T T	
D_Stru	C A C	G - - T	C C T C G	A C C T T	G C G T T G G A T G T	C C C - - - - - - - - A G	T T A A	G T G	C A C C	G A T	T T T	
DK_Sus	C A C	G G A T	C T T T G	A C T T T	G G G T T G G C T A T	C C C T C G T T T G A G	T C A A	G C G	C G A C	G T T	T T T	
E_Art	C A C	G G A T	C T T T G	A C T T T	G G G T T G G C T A T	C C C T C G T T T G A G	T C A A	G C G	C G A C	G T T	T T T	
F_Bro	C A C	G G A T	C T T T G	A C T T T	G G G T T G G C T A T	C C C T C G T T T G A G	T C A A	G C G	C G A C	G T T	T T T	
F_Bur	C A C	G - - T	C C T C G	A C C T T	G C G T T G G A T G T	C C C - - - - - - - - A G	T T A A	G T G	C A C C	G A T	T T T	
H_Mat	C A C	G - - T	C C T C G	A C C T T	G C G T T G G A T G T	C C C - - - - - - - - A G	T T A A	G T G	C A C C	G A T	T T T	
HR_Plit2	C A C	G - - T	C C T C G	A C C T T	G C G T T G G A T G T	C C C - - - - - - - - A G	T T A A	G T G	C A C C	G A T	T T T	
I_Abr1	C A C	G - - T	C C T C G	A C C T T	G C G T T G G A T G T	C C C - - - - - - - - A G	T T A A	G T G	C A C C	G A T	T T T	
I_Abr2	C A C	G - - T	C C T C G	A C C T T	G C G T T G G A T G T	C C C - - - - - - - - A G	T T A A	G T G	C A C C	G A T	T T T	
I_Gar	C A C	G G A T	C T T T G	A C T T T	G G G T T G G C T A T	C C C T C G T T T G A G	T C A A	G C G	C G A C	G T T	T T T	
PL_Jab1	C A C	G - - T	C C T C G	A C C T T	G C G T T G G A T G T	C C C - - - - - - - - A G	T T A A	G T G	C A C C	G A T	T T T	
PL_Mik	C A C	G - - T	C C T C G	A C C T T	G C G T T G G A T G T	C C C - - - - - - - - A G	T T A A	G T G	C A C C	G T T	T A T	
RO_Fag	C A C	G - - T	C C T C G	A C C T T	G C G T T G G A T G T	C C C - - - - - - - - A G	T T A A	G T G	C A C C	G T T	T T T	
RO_Meh	C A C	G - - T	C C T C G	A C C T T	G C G T T G G A T G T	C C C - - - - - - - - A G	T T A A	G T G	C A C C	G A T	T T T	
RO_Sem	C A C	G - - T	C C T C G	A C C T T	G C G T T G G A T G T	C C C - - - - - - - - A G	T T A A	G T G	C A C C	G A T	T T T	
RO_Sin	C A C	G - - T	C C T C G	A C C T T	G C G T T G G A T G T	C C C - - - - - - - - A G	T T A A	G T G	C A C C	G A T	T T T	
S_Bis	C A T	G - - T	C C T C G	A C C T T	G C G T T G G A T G T	C G C - - - - - - - - A G	T T A A	G T G	C A C C	G A T	T T T	
SK_Kov	C A C	G - - T	C C T C G	A C C T T	G C G T T G G A T G T	C C C - - - - - - - - A G	T T A A	G T G	C A C C	G A T	T T T	
SK_Slo	C A C	G - - T	C C T C G	A C C T T	G C G T T G G A T G T	C C C - - - - - - - - A G	T T A A	G T G	C A C C	G A T	T T T	
SLO_Trn	C A C	G - - T	C C T C G	A C C T T	G C G T T G G A T G T	C C C - - - - - - - - A G	T T A A	G T G	C A C C	G A T	T T T	
UK_Krim	C A C	G - - T	C C T C G	A C C T T	G C G T T G G A T G T	C C C - - - - - - - - A G	T T A A	G T G	C A C C	G A T	T T T	

TABLE 7.2.2. Alignment of *Fomes fomentarius* elongation factor alpha 1 (efa) sequences. Overall, we found 38 variable positions comprised of two indels and 36 additional heterozygous positions. Variable positions are grey shaded.

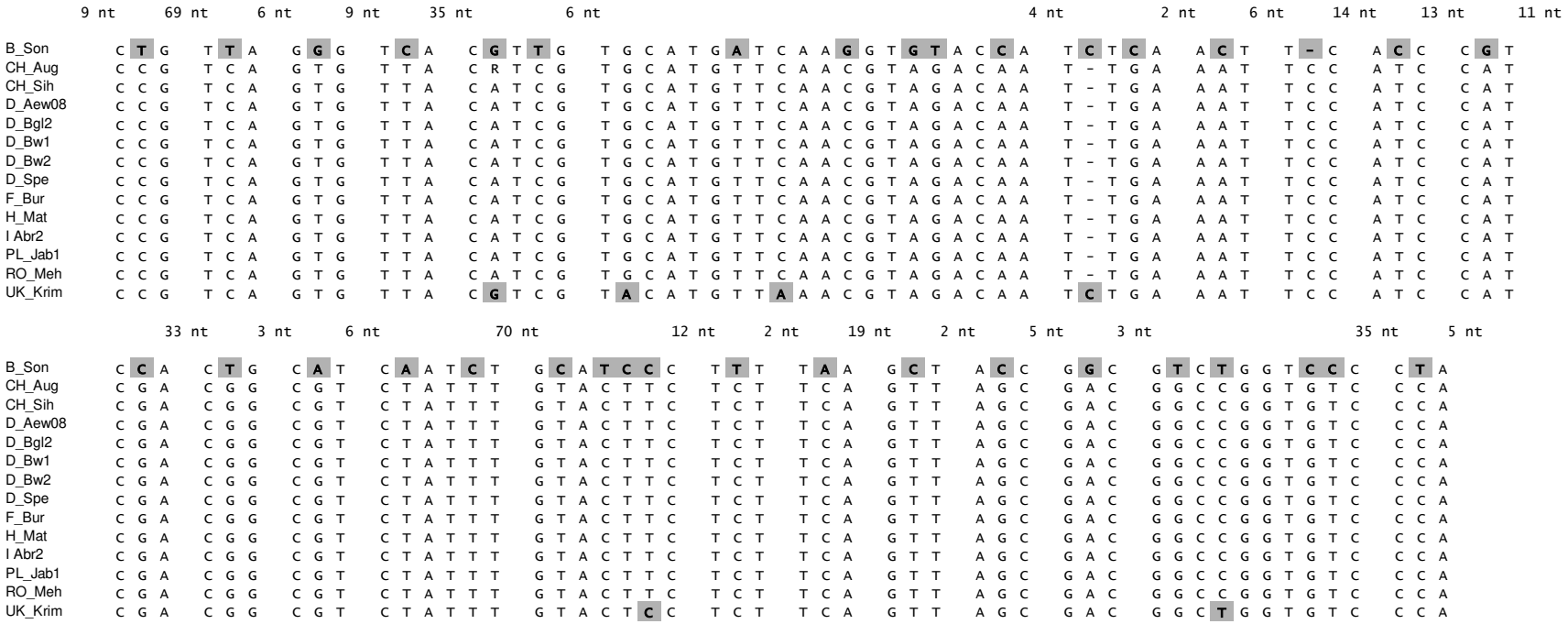

TABLE 7.2.3. List of coordinates, principal components of temperature (PC Temp) and precipitation (PC Prec), habitat amount (Fruitbody biomass and Forest cover) and forest management of 61 sites with samples of Fomes fomentarius throughout Europe. PC1 and PC2 refer to the first and second principal components of temperature and precipitation.

ID	Plot_name	Country	Lat	Lon	PC1 Temp	PC2 Temp	PC1 Prec	PC2 Prec	Fruitbody biomass [g]	Forest cover	Management
1	A_Ges01	Austria	47.5327	14.6397	-2.91	0.32	2.78	1.88	2624	0.70	unmanaged
2	A_Ges02	Austria	47.6096	14.7307	-1.97	1.91	1.17	2.20	607	0.70	unmanaged
3	AL_Ver	Albania	42.6294	19.7341	0.07	-1.56	2.85	-1.52	1490	0.62	managed
4	B_Son	Belgium	50.7509	4.4192	2.75	-0.19	-0.98	-2.19	1659	0.86	unmanaged
5	BUL_Boa	Bulgaria	42.8168	24.2638	-1.04	2.17	-2.27	-0.01	1318	0.90	unmanaged
6	CH_Aug	Switzerland	46.7022	7.6322	0.95	0.84	0.47	-0.46	904	0.49	managed
7	CH_See	Switzerland	46.9781	9.6198	-0.69	-0.24	2.10	1.56	4261	0.88	unmanaged
8	CH_Waa	Switzerland	46.6695	6.6169	0.94	1.19	1.35	-1.96	844	0.90	managed
9	D_Aew08	Germany	48.3826	9.3824	-0.03	0.25	0.39	0.23	527	0.89	managed
10	D_Bgl1	Germany	47.5226	12.9400	-2.28	0.70	3.80	1.82	2263	0.67	unmanaged
11	D_Bgl2	Germany	47.5475	12.9635	-0.92	2.45	3.34	1.98	2308	0.82	unmanaged
12	D_Bw1	Germany	49.0220	13.3870	-2.81	-2.02	3.03	-0.85	5395	0.84	unmanaged
13	D_Bw2	Germany	48.5507	13.4224	-0.44	2.94	0.97	-0.61	1249	0.84	managed
14	D_Hew12	Germany	51.1007	10.4552	0.35	0.38	-2.75	-0.67	233	0.87	unmanaged
15	D_Kem	Germany	50.0970	9.4620	0.96	1.64	-2.45	-1.00	2061	0.71	managed
16	D_Onw	Germany	48.0917	10.3446	-0.23	0.41	0.40	0.86	3007	0.93	unmanaged
17	D_Rot	Germany	49.3808	10.2478	0.21	0.78	-1.60	-0.66	1483	0.46	unmanaged
18	D_Sew07	Germany	53.1074	13.6944	0.58	0.54	-3.70	-0.48	825	0.88	unmanaged
19	D_Soed	Germany	50.3944	8.8036	1.54	1.55	-2.64	-1.52	1149	0.02	unmanaged
20	D_Spe	Germany	49.8902	9.3507	0.90	1.42	-1.87	-1.04	3127	0.89	unmanaged
21	D_Stru	Germany	50.7630	8.2370	1.55	-1.38	-0.89	-1.92	1590	0.89	managed
22	DK_Lin	Denmark	55.2040	8.9510	1.52	-2.93	-0.94	-0.17	990	0.17	unmanaged
23	DK_Sus	Denmark	55.3780	11.5670	1.33	-2.85	-3.85	-0.75	1223	0.30	unmanaged
24	E_Art	Spain	43.2122	-1.7986	6.40	1.02	4.12	-0.96	740	0.84	unmanaged
25	H_Mat	Hungary	47.8743	20.0054	-2.47	-0.33	-1.27	1.17	1932	0.88	unmanaged
26	HR_Plit1	Croatia	44.8650	15.5852	0.89	0.01	4.37	-1.10	550	0.94	unmanaged
27	HR_Plit2	Croatia	44.8891	15.5535	0.64	-0.33	4.53	-1.21	1198	0.94	unmanaged
28	I_Abr1	Italy	41.7520	13.8163	1.77	-2.28	-1.30	-0.70	1697	0.90	managed
29	I_Bel	Italy	46.4500	12.4700	-2.90	0.37	-0.33	2.42	395	0.44	managed
30	I_Gar	Italy	41.8246	15.9937	5.08	-0.86	-3.04	-1.20	4489	0.97	unmanaged
31	I_Kal10	Italy	39.8910	15.9314	7.21	1.18	-1.63	1.34	4077	0.20	managed
32	PL_Jab1	Poland	49.2800	22.3003	-3.50	-0.15	-0.79	1.39	2547	0.89	managed
33	PL_Mik	Poland	49.2747	22.1854	-3.75	-0.61	-0.41	1.34	1807	0.87	managed
34	RO_Bel	Romania	45.6399	24.9664	-3.97	-2.52	0.42	2.38	3975	0.88	unmanaged
35	RO_Boi	Romania	45.5561	24.4193	-2.77	-0.24	-0.67	2.38	2165	0.91	unmanaged
36	RO_Fag	Romania	45.6676	25.1705	-2.78	0.90	-1.19	2.53	544	0.92	unmanaged
37	RO_Meh	Romania	44.9572	22.5126	-0.86	0.85	-0.46	1.18	2337	0.83	unmanaged
38	RO_Run	Romania	45.2567	23.1195	-0.86	1.66	-1.17	1.49	1146	0.93	unmanaged
39	RO_Sem	Romania	45.1616	22.0654	-2.41	-2.18	2.33	2.27	1899	0.91	unmanaged
40	RO_Sin	Romania	45.6970	25.1670	-2.00	2.91	-2.51	2.45	2065	0.78	unmanaged
41	S_Bis	Sweden	56.8014	12.8896	-0.21	-1.71	-0.73	-0.27	1420	0.79	unmanaged

TABLE 7.2.3 (continued). List of coordinates, principal components of temperature (PC Temp) and precipitation (PC Prec), habitat amount (Fruitbody biomass and Forest cover) and forest management of 61 sites with samples of Fomes fomentarius throughout Europe. PC1 and PC2 refer to the first and second principal components of temperature and precipitation.

ID	Plot_name	Country	Lat	Lon	PC1 Temp	PC2 Temp	PC1 Prec	PC2 Prec	Fruitbody biomass [g]	Forest cover	Management
42	S_Soed	Sweden	56.0365	13.2343	0.35	-2.18	-2.15	-0.64	1123	0.84	unmanaged
43	S_Tor	Sweden	55.5558	13.2221	1.11	-1.99	-3.15	-0.81	1519	0.86	managed
44	SK_Kov	Slovakia	48.6419	19.0642	-2.04	1.99	-0.90	0.32	4405	0.93	managed
45	SK_Slo	Slovakia	48.9220	20.3920	-3.22	-0.69	-0.58	2.23	2679	0.82	unmanaged
46	SLO_Boc	Slovenia	46.2750	15.6511	-1.27	1.38	1.48	0.66	2191	0.89	unmanaged
47	SLO_Sto	Slovenia	45.6235	14.8159	0.34	-0.22	4.51	-1.19	1216	0.86	unmanaged
48	SLO_Trn	Slovenia	45.9894	13.8109	-0.87	-1.37	3.09	-0.30	1693	0.88	managed
49	UK_Kar	Ukraine	48.6866	23.0437	-1.25	1.95	-1.59	0.68	1547	0.77	managed
50	UK_Krim	Ukraine	44.7417	34.3417	0.30	0.63	-1.13	-0.66	2877	0.87	managed
51	UK_Uho1	Ukraine	48.2941	23.6527	-3.04	-0.79	0.04	1.50	2166	0.91	unmanaged
52	UK_Uho2	Ukraine	48.2714	23.6317	-1.87	1.15	-0.84	1.01	1200	0.92	unmanaged
53	F_Bro	France	43.0448	0.2744	2.28	1.31	0.13	-1.99	3049	0.27	managed
54	F_Bur	France	42.8719	0.6648	-0.05	-1.95	2.63	-1.95	1896	0.91	managed
55	F_Fon	France	48.3756	2.6233	3.29	1.68	-2.70	-2.29	21728	0.77	managed
56	F_Gue	France	44.0243	3.4403	1.16	0.15	-0.65	-1.84	3933	0.88	managed
57	F_Mas	France	42.4742	3.0197	4.65	0.24	-0.80	-1.10	7230	0.60	unmanaged
58	F_Mc	France	45.4789	2.7998	-0.13	-1.28	0.38	-0.90	8892	0.32	managed
59	F_Nor	France	48.8231	-1.0302	4.33	-1.92	-0.60	-1.44	7616	0.87	managed
60	F_Vos	France	47.9257	6.9217	-0.52	-3.56	5.13	-2.40	8577	0.67	managed
61	I_Abr2	Italy	41.7861	13.7711	2.59	-0.54	-1.27	-0.52	2733	0.73	managed

TABLE 7.2.4. Loadings on principal components by the 19 bioclimatic variables for temperature and precipitation. Explained variance of principal components is noted in brackets.

	Temperature		Precipitation	
	PC1 (53 %)	PC2 (22 %)	PC1 (64 %)	PC2 (27 %)
BIO 1	0.38	0.22	-	-
BIO 2	-0.19	0.45	-	-
BIO 3	0.08	0.24	-	-
BIO 4	-0.31	0.25	-	-
BIO 5	0.24	0.50	-	-
BIO 6	0.41	-0.03	-	-
BIO 7	-0.32	0.36	-	-
BIO 8	-0.12	0.34	-	-
BIO 9	0.35	-0.04	-	-
BIO 10	0.30	0.36	-	-
BIO 11	0.41	0.04	-	-
BIO 12	-	-	0.44	-0.02
BIO 13	-	-	0.38	0.31
BIO 14	-	-	0.40	-0.24
BIO 15	-	-	-0.03	0.65
BIO 16	-	-	0.39	0.29
BIO 17	-	-	0.39	-0.29
BIO 18	-	-	0.29	0.39
BIO 19	-	-	0.33	-0.32

TABLE 7.2.5. Pearson´s coefficients of correlation between principal components of climate and latitude/longitude.

	Latitude	Longitude
Temperature PC1	-0.19	-0.59
Temperature PC2	-0.23	0.13
Precipitation PC1	-0.33	-0.14
Precipitation PC2	-0.06	0.64

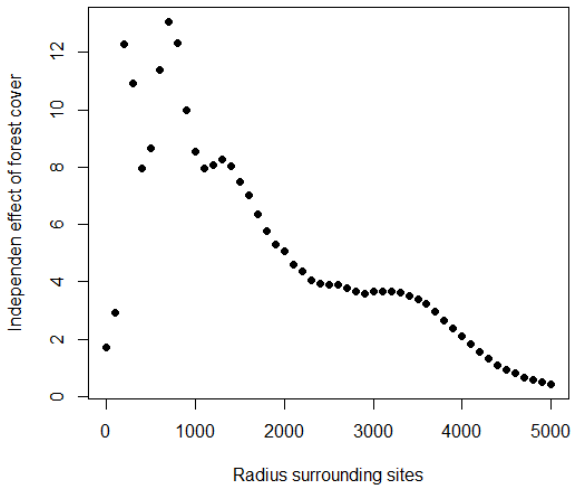

FIGURE 7.2.2. Independent effect in percent of forest cover on alpha-diversity of all species from the fruitbodies after hierarchical partitioning based on a generalized linear model (quasipoisson-family) in relation to the radius surrounding the sites used for calculating forest cover. For each calculation we increased the radius by 100 m. The independent effect of forest cover peaked at 700 m, which was then chosen as the radius for calculating the forest cover for all further analyses.

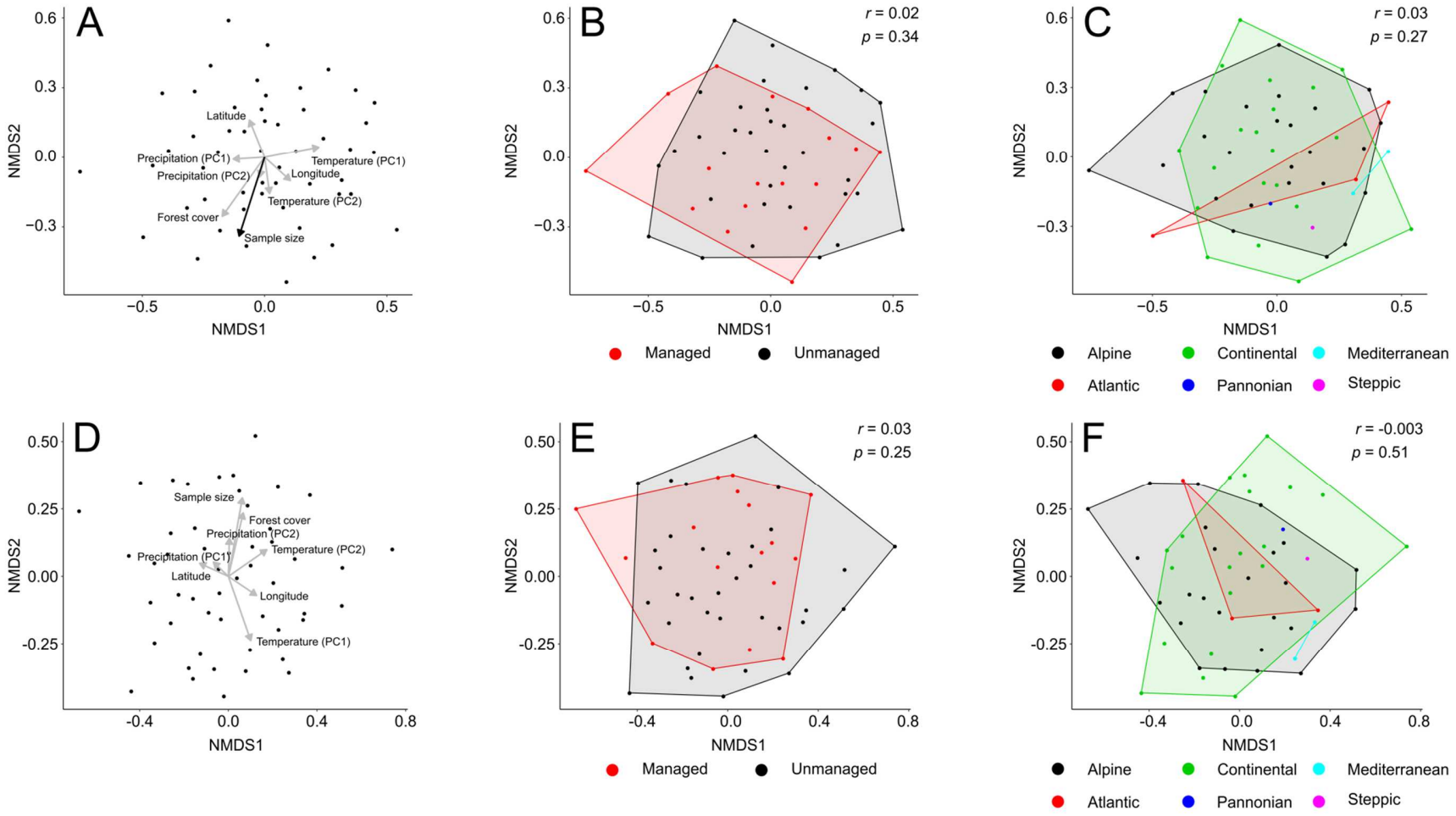

FIGURE 7.2.3. Multivariate analysis of the community composition of all species (A, B, C) and fungi specialists (D, E, F). Axes show the scores of a non-metric multidimensional scaling (NMDS) of the community composition (k = 2, all species: stress = 0.29; fungi specialists: stress = 0.27). A, D: Environmental vectors were fitted to the ordination axes; significant effects are given in bold arrows. Except for a correlation between sample size and the ordination axes for all species ($P < 0.05$, $r^2 = 0.13$) no correlations between environmental predictors and the ordination axes were significant ($P > 0.05$) for both, all species and fungi specialists. B, E: Group comparison between managed (red area and points) and unmanaged (black area and points) sites. There was no significant difference in community composition between management types for all species (ANOSIM: $r = 0.02$, $P > 0.1$, based on 9999 permutations) and for fungi specialists (ANOSIM: $r = 0.03$, $P > 0.1$, based on 9999 permutations). C, F: Group comparison between biogeographic zones (see legend below the graphic for color explanations). There was no significant difference in community composition across biogeographic zones for all species (ANOSIM: $r = 0.03$, $P > 0.1$, based on 9999 permutations) and for fungi specialists (ANOSIM: $r = -0.003$, $P > 0.1$, based on 9999 permutations).

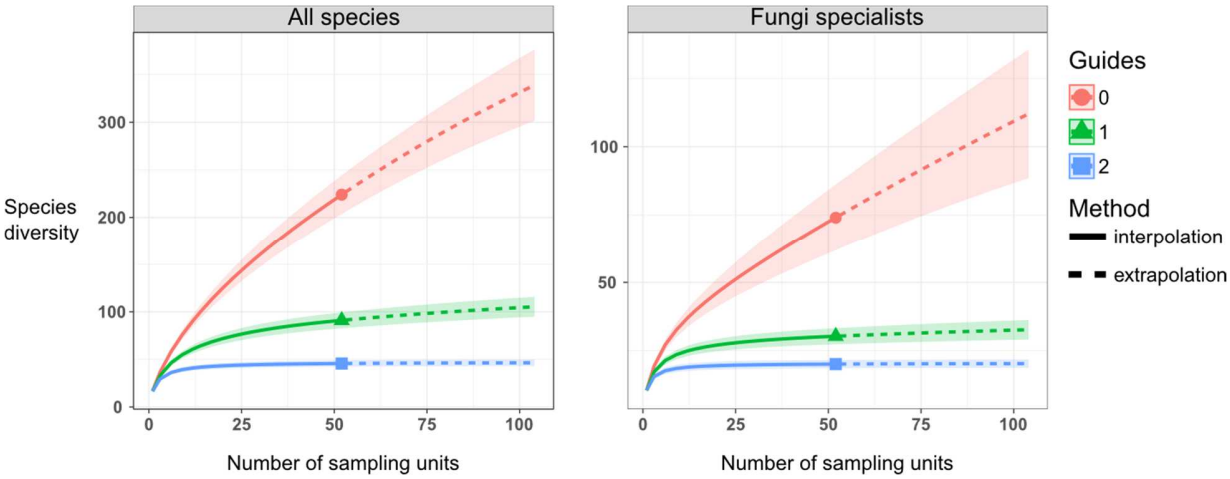

FIGURE 7.2.4. Extrapolation curves of species diversity against the number of sampling units based on Hill numbers of the orders 0 (red line and circle), 1 (green line and triangle) and 2 (blue line and square) for all species and the fungi specialists

TABLE 7.2.5. Coefficients of the I-splines from the GDM of overall beta diversity, turnover and nestedness of the fungi specialist species. Significant or marginally significant *P*-values for the I-splines of the predictor variables after 999 permutations are given in bold.

Explanatory matrix	Predictor set	Predictor	I-Spline 1	I-Spline 2	I-Spline 3	Sum of coefficients	*P*
Overall beta	Space	Latitude	0.134	0	0.	0.134	0.14
		Longitude	0	0.065	0	0.065	0.38
	Climate	Temperature (PC1)	0	0	0	0	0.99
		Temperature (PC2)	0	0	0	0	0.99
		Precipitation (PC1)	0	0	0	0	0.99
		Precipitation (PC2)	0.035	0	0	0.035	0.51
	Habitat amount	Forest cover	0	0.035	0	0.035	0.56
		Sample size	0.150	0	0	0.150	0.11
Turnover	Space	Latitude	0.157	0	0	0.157	0.14
		Longitude	0.010	0.064	0	0.074	0.35
	Climate	Temperature (PC1)	0	0	0	0	0.97
		Temperature (PC2)	0	0	0.018	0.018	0.68
		Precipitation (PC1)	0	0	0.026	0.026	0.58
		Precipitation (PC2)	0	0	0	0	0.98
	Habitat amount	Forest cover	0	0.057	0.054	0.112	0.38
		Sample size	0.058	0	0	0.058	0.48
Nestedness	Space	Latitude	0	0	0.045	0.045	0.26
		Longitude	0	0	0	0	0.97
	Climate	Temperature (PC1)	0.061	0	0	0.061	0.18
		Temperature (PC2)	0	0	0	0	0.96
		Precipitation (PC1)	0	0	0	0	0.95
		Precipitation (PC2)	0.031	0	0	0.031	0.35
	Habitat amount	Forest cover	0.031	0	0	0.031	0.46
		Sample size	0.050	0	0	0.050	0.31

TABLE 7.2.6. Coefficients of the I-splines from the GDM of overall beta diversity, turnover and nestedness of the consumer species. Significant or marginally significant *P*-values for the I-splines of the predictor variables after 999 permutations are given in bold.

Explanatory matrix	Predictor set	Predictor	I-Spline 1	I-Spline 2	I-Spline 3	Sum of coefficients	*P*
Overall beta	Space	Latitude	0.120	0	0	0.120	0.21
		Longitude	0	0.085	0	0.085	0.38
	Climate	Temperature (PC1)	0	0	0	0	0.99
		Temperature (PC2)	0	0	0.012	0.012	0.70
		Precipitation (PC1)	0	0	0	0	0.99
		Precipitation (PC2)	0.100	0	0	0.100	0.18
	Habitat amount	Forest cover	0	0	0	0	0.99
		Sample size	0.121	0	0	0.121	0.25
Turnover	Space	Latitude	0.124	0	0	0.124	0.16
		Longitude	0	0.012	0.131	0.143	0.20
	Climate	Temperature (PC1)	0	0	0	0	0.98
		Temperature (PC2)	0	0	0.045	0.045	0.50
		Precipitation (PC1)	0	0	0	0	0.98
		Precipitation (PC2)	0	0	0	0	0.98
	Habitat amount	Forest cover	0	0	0.053	0.053	0.62
		Sample size	0.020	0.014	0	0.034	0.65
Nestedness	Space	Latitude	0	0	0.033	0.033	0.34
		Longitude	0.045	0	0	0.045	0.35
	Climate	Temperature (PC1)	0.038	0	0	0.038	0.29
		Temperature (PC2)	0	0	0	0	0.98
		Precipitation (PC1)	0	0	0	0	0.96
		Precipitation (PC2)	0.056	0	0	0.056	0.18
	Habitat amount	Forest cover	0.071	0	0	0.071	0.26
		Sample size	0.044	0	0	0.044	0.27

TABLE 7.2.7. Coefficients of the I-splines from the GDM of overall beta diversity, turnover and nestedness of the predator species. Significant or marginally significant *P*-values for the I-splines of the predictor variables after 999 permutations are given in bold.

Explanatory matrix	Predictor set	Predictor	I-Spline 1	I-Spline 2	I-Spline 3	Sum of coefficients	*P*
Overall beta	Space	Latitude	**1.850**	**0.071**	**0.190**	**2.110**	**0.05**
		Longitude	0	0	0.573	0.573	0.46
	Climate	Temperature (PC1)	0.610	0	0	0.610	0.38
		Temperature (PC2)	0	0	0.400	0.400	0.43
		Precipitation (PC1)	0.191	0.044	0.046	0.281	0.62
		Precipitation (PC2)	0.210	0	0.220	0.430	0.51
	Habitat amount	Forest cover	1.233	0	0	1.233	0.26
		Sample size	**2.668**	**0**	**0.239**	**2.910**	**0.01**
Turnover	Space	Latitude	**2.070**	**0**	**0.289**	**2.359**	**0.04**
		Longitude	0	0	0.069	0.069	0.76
	Climate	Temperature (PC1)	0.800	0	0	0.800	0.26
		Temperature (PC2)	0	0	0.230	0.230	0.61
		Precipitation (PC1)	0.397	0	0.246	0.643	0.36
		Precipitation (PC2)	0	0	0.440	0.440	0.35
	Habitat amount	Forest cover	1.203	0	0	1.203	0.24
		Sample size	**2.546**	**0**	**0.367**	**2.912**	**0.02**
Nestedness	Space	Latitude	0	0	0	0	-
		Longitude	0	0	0	0	-
	Climate	Temperature (PC1)	0	0	0	0	-
		Temperature (PC2)	0	0	0	0	-
		Precipitation (PC1)	0	0	0	0	-
		Precipitation (PC2)	0	0	0	0	-
	Habitat amount	Forest cover	0	0	0	0	-
		Sample size	0	0	0	0	-

TABLE 7.2.8. Coefficients of the I-splines from the GDM of overall beta diversity, turnover and nestedness of the parasitoid species. Significant or marginally significant *P*-values for the I-splines of the predictor variables after 999 permutations are given in bold.

Explanatory matrix	Predictor set	Predictor	I-Spline 1	I-Spline 2	I-Spline 3	Sum of coefficients	*P*
Overall beta	Space	Latitude	**1.590**	**0**	**1.890**	**3.474**	**0.03**
		Longitude	0.126	0	0.123	0.249	0.65
	Climate	Temperature (PC1)	0	0	0.790	0.790	0.62
		Temperature (PC2)	0	0	0.901	0.901	0.16
		Precipitation (PC1)	0	0	0.225	0.225	0.55
		Precipitation (PC2)	0.069	0	0.425	0.494	0.42
	Habitat amount	Forest cover	0	0.149	0	0.149	0.68
		Sample size	0.052	0	1.245	1.297	0.19
Turnover	Space	Latitude	**0.829**	**0**	**1.925**	**2.764**	**0.04**
		Longitude	0.140	0	0.429	0.569	0.39
	Climate	Temperature (PC1)	0	0	0.980	0.980	0.53
		Temperature (PC2)	0	0	0.490	0.490	0.36
		Precipitation (PC1)	0	0	0.055	0.055	0.70
		Precipitation (PC2)	0	0	0.488	0.488	0.39
	Habitat amount	Forest cover	0	0.415	0	0.415	0.59
		Sample size	0.010	0	1.317	1.327	0.154
Nestedness	Space	Latitude	0	0	0	0	-
		Longitude	0	0	0	0	-
	Climate	Temperature (PC1)	0	0	0	0	-
		Temperature (PC2)	0	0	0	0	-
		Precipitation (PC1)	0	0	0	0	-
		Precipitation (PC2)	0	0	0	0	-
	Habitat amount	Forest cover	0	0	0	0	-
		Sample size	0	0	0	0	-

Abundance-based analysis of beetle data

Methods

Beetles reared from *Fomes fomentarius* fruitbodies were identified by classic keys and thus offered reliable abundance information for each sample in contrast to data gained through metabarcoding. Furthermore, beetles could be identified from nine sites in France and Italy where lab problems impeded metabarcoding. Hence, we decided to perform additional analyses based on abundance-data for this arthropod group over all available 61 sites (see Figure 2.3.1).

Besides the analyses performed for the overall arthropod data, we calculated the abundance of beetles as the sum of individuals per site and included this measure ($\log_e$-transformed) in our generalised linear model of alpha-diversity of the sites. This way we can test whether the effect of sample size (i.e. biomass of sampled fruitbodies) is present when we account for the positive effect of more-individuals on local alpha-diversity (Müller et al. 2018). Furthermore, we repeated the generalized dissimilarity modelling (GDM) approach based on the abundance-based dissimilarity metrics in order the get a more nuanced view on the effect of space, climate and habitat on the beta-diversity in beetles occurring in fruitbodies. We therefore calculated Bray-Curtis-dissimilarities and decomposed it into the two components based on balanced variation in abundance and dissimilarity introduced by abundance gradients (Baselga 2013). All calculations were performed once for all beetles and once for fungi specialists. In all other aspects the modelling procedure was the

same as with the Sørensen-dissimilarity metrics of the overall arthropod communities.

Results

Identification of reared beetles from fruitbodies sampled at 61 sites resulted in 44,518 individuals of 123 species (see Digital Supplementary). The strongest predictor of the number of species was sample size (weight of the fruitbody), even after including the number of individuals into the models (Table 7.2.9). The importance of sample size was also confirmed by the relative importance of variables linked to habitat amount in explaining alpha-diversity as suggested by hierarchical partitioning on the variable sets (Fig. 7.2.5). Here, forest cover and sample size alone explained approximately 50 % of the variation in alpha-diversity for all beetle species and the largest proportion of variation for fungi specialists.

Generalized dissimilarity models based on presence-absence data showed that dissimilarity in longitude and sample size had a significant effect on the Sorensen-dissimilarity of the overall beetle community and fungi specialists. Variables linked to habitat amount explained the largest fraction of deviance in the overall models, next to a large proportion jointly explained by space, climate and habitat amount (Fig. 7.2.5). Here, changes in the rate of turnover among sites were significantly affected by dissimilarity in longitude, while dissimilarity due to nestedness was affected by dissimilarity in sample size (Table 7.2.10 and 7.2.11). Generalized dissimilarity models based on abundance data confirmed these results (Table 7.2.12 and 7.2.13). Variables linked to habitat amount explained most of the deviance in the models based on Sorensen and Bray-Curtis dissimilarities as well as nestedness and changes due to abundance gradients (Fig. 7.2.5). Variables linked to space explained most of the deviance in the models of species turnover and balanced changes in abundance (Fig. 7.2.5).

TABLE 7.2.9. Z-values and explained deviance of generalized linear models (quasipoisson-family) with the number of species of all species or fungi specialists as response variables. Models were calculated once without and once with the number of individuals per site (log_e-transformed) as predictor. Significant effects are indicated by bold typesetting. PC1 and PC2 refer to the first two axes of the respective principal component analyses of temperature or precipitation variables (see *Methods*).

Predictor set	Predictor	All species		Fungi specialists	
Individuals	Individuals	---	1.58	---	**2.25** *
Space	Latitude	-0.09	0.28	0.39	0.85
	Longitude	-1.18	-1.13	-0.13	-0.11
Climate	Temperature (PC1)	**-1.88** .	-1.57	-0.84	-0.42
	Temperature (PC2)	0.33	0.29	1.50	1.45
	Precipitation (PC1)	-0.56	-0.21	0.28	0.75
	Precipitation (PC2)	-1.37	-1.10	-0.04	0.32
Habitat amount	Forest cover	0.21	0.08	0.49	0.40
	Sample size	**7.35** ***	**4.72** ***	**4.15** ***	**2.18** *
Explained deviance		0.59	0.61	0.28	0.35

TABLE 7.2.10. Coefficients of three I-splines (i.e. 1, 2 and 3) from the GDM of overall beta-diversity (β_{Sor}), turnover (β_{Sim}) and nestedness (β_{Sne}) of all beetle species.

Response matrix	Predictor set	Predictor	I-Spline			Sum of coefficients	*P*
			1	2	3		
Sorensen-dissimilarity	Space	Latitude	0.036	0	0	0.036	0.60
		Longitude	**0.326**	**0.079**	**0.093**	**0.498**	**0.01**
	Climate	Temperature (PC1)	0	0	0	0	0.98
		Temperature (PC2)	0.073	0	0.028	0.101	0.40
		Precipitation (PC1)	0	0	0	0	0.98
		Precipitation (PC2)	0	0	0	0	0.98
	Habitat amount	Forest cover	0.144	0	0	0.144	0.26
		Sample size	**0.060**	**0**	**0.931**	**0.991**	**<0.01**
Turnover component	Space	Latitude	0.115	0	0	0.115	0.26
		Longitude	**0.433**	**0**	**0.202**	**0.635**	**<0.01**
	Climate	Temperature (PC1)	0	0	0	0	0.98
		Temperature (PC2)	0	0.011	0.099	0.110	0.25
		Precipitation (PC1)	0	0	0	0	0.98
		Precipitation (PC2)	0	0	0	0	0.98
	Habitat amount	Forest cover	0	0.124	0.091	0.216	0.15
		Sample size	0	0.013	0	0.013	0.75
Nestedness component	Space	Latitude	0	0	0.069	0.069	0.16
		Longitude	0	0	0	0	0.99
	Climate	Temperature (PC1)	0.049	0	0	0.049	0.23
		Temperature (PC2)	0.006	0	0	0.006	0.69
		Precipitation (PC1)	0	0	0.067	0.067	0.12
		Precipitation (PC2)	0.040	0	0	0.040	0.29
	Habitat amount	Forest cover	0.047	0	0	0.047	0.31
		Sample size	**0.063**	**0**	**0.257**	**0.320**	**<0.01**

Notes. Significant ($P < 0.05$) or marginally significant ($P < 0.1$) *P*-values for the I-splines of the predictor variables after 999 permutations are given in bold. PC1 and PC2 refer to the first two axes of the respective principal component analyses of temperature or precipitation variables (see *Methods*).

TABLE 7.2.11. Coefficients of three I-splines (i.e. 1, 2 and 3) from the GDM of overall beta-diversity (β_{Sor}), turnover (β_{Sim}) and nestedness (β_{Sne}) of beetle species categorized as fungi specialists.

Response matrix	Predictor set	Predictor	I-Spline			Sum of coefficients	*P*
			1	2	3		
Sorensen-dissimilarity	Space	Latitude	0.026	0	0	0.026	0.60
		Longitude	**0.213**	**0.072**	**0.020**	**0.305**	**0.02**
	Climate	Temperature (PC1)	0	0	0	0	0.98
		Temperature (PC2)	0	0	0.076	0.254	0.25
		Precipitation (PC1)	0	0	0	0	0.97
		Precipitation (PC2)	0	0	0	0	0.99
	Habitat amount	Forest cover	0.084	0.012	0.009	0.105	0.32
		Sample size	**0.157**	**0.003**	**0.374**	**0.534**	**0.04**
Turnover component	Space	Latitude	0.047	0	0	0.047	0.55
		Longitude	**0.333**	**0.017**	**0.076**	**0.426**	**0.01**
	Climate	Temperature (PC1)	0	0	0	0	0.99
		Temperature (PC2)	0	0	0.107	0.107	0.18
		Precipitation (PC1)	0	0	0	0	0.99
		Precipitation (PC2)	0	0	0.007	0.007	0.73
	Habitat amount	Forest cover	0	0.080	0.073	0.153	0.27
		Sample size	0.095	0.044	0	0.139	0.23
Nestedness component	Space	Latitude	0	0	0.069	0.069	0.18
		Longitude	0	0	0	0	1.00
	Climate	Temperature (PC1)	0.049	0	0	0.049	0.23
		Temperature (PC2)	0.006	0	0	0.006	0.69
		Precipitation (PC1)	0	0	0.067	0.067	0.14
		Precipitation (PC2)	0.040	0	0	0.040	0.35
	Habitat amount	Forest cover	0.047	0	0	0.047	0.34
		Sample size	**0.063**	**ß**	**ß-257**	**0.320**	**0.01**

Notes. Significant ($P < 0.05$) or marginally significant ($P < 0.1$) *P*-values for the I-splines of the predictor variables after 999 permutations are given in bold. PC1 and PC2 refer to the first two axes of the respective principal component analyses of temperature or precipitation variables (see *Methods*).

TABLE 7.2.12. Coefficients of three I-splines (i.e. 1, 2 and 3) from the GDM of abundance-based beta-diversity (Bray-Curtis dissimilarity) and its components dissimilarity due to balanced changes in abundance and dissimilarity due to abundance gradients of all beetle species.

Response matrix	Predictor set	Predictor	I-Spline			Sum of coefficients	*P*
			1	2	3		
Bray-Curtis dissimilarity	Space	Latitude	0.228	0	0	0.228	0.31
		Longitude	**0.482**	**0**	**0**	**0.482**	**0.06**
	Climate	Temperature (PC1)	0	0	0	0	0.99
		Temperature (PC2)	0.029	0	0.026	0.055	0.70
		Precipitation (PC1)	0	0	0	0	0.98
		Precipitation (PC2)	0.218	0	0	0.218	0.29
	Habitat amount	Forest cover	0	0.347	0	0.347	0.21
		Sample size	**0.220**	**0.945**	**0.728**	**1.893**	**<0.01**
Balanced changes	Space	Latitude	0.077	0	0	0.077	0.52
		Longitude	**0.373**	**0**	**0**	**0.373**	**0.03**
	Climate	Temperature (PC1)	0	0	0	0	0.97
		Temperature (PC2)	**0.239**	**0**	**0.165**	**0.404**	**0.08**
		Precipitation (PC1)	0	0	0	0	0.97
		Precipitation (PC2)	0	0	0.073	0.073	0.42
	Habitat amount	Forest cover	0	0.284	0.147	0.432	0.10
		Sample size	0	0	0	0	0.99
Abundance-gradients	Space	Latitude	0.011	0	0	0.011	0.72
		Longitude	0	0	0.029	0.029	0.71
	Climate	Temperature (PC1)	0.064	0	0	0.064	0.47
		Temperature (PC2)	0	0	0	0	0.96
		Precipitation (PC1)	0	0	0.070	0.070	0.47
		Precipitation (PC2)	0.064	0	0	0.064	0.50
	Habitat amount	Forest cover	0.032	0	0	0.032	0.69
		Sample size	**0.068**	**0.463**	**0.085**	**0.616**	**<0.01**

Notes. Significant ($P < 0.05$) or marginally significant ($P < 0.1$) *P*-values for the I-splines of the predictor variables after 999 permutations are given in bold. PC1 and PC2 refer to the first two axes of the respective principal component analyses of temperature or precipitation variables (see *Methods*).

TABLE 7.2.13. Coefficients of three I-splines (i.e. 1, 2 and 3) from the GDM of abundance-based beta-diversity (Bray-Curtis dissimilarity) and its components dissimilarity due to balanced changes in abundance and dissimilarity due to abundance gradients of beetle species categorized as fungi specialists.

Response matrix	Predictor set	Predictor	I-Spline			Sum of coefficients	*P*
			1	2	3		
Bray-Curtis dissimilarity	Space	Latitude	0.235	0	0	0.235	0.32
		Longitude	**0.461**	**0**	**0**	**0.461**	**0.08**
	Climate	Temperature (PC1)	0	0	0	0	0.98
		Temperature (PC2)	0.025	0	0.025	0.050	0.69
		Precipitation (PC1)	0	0	0	0	0.98
		Precipitation (PC2)	0.221	0	0	0.221	0.29
	Habitat amount	Forest cover	0	0.345	0	0.345	0.18
		Sample size	**0.212**	**0.937**	**0.714**	**1.863**	**<0.01**
Balanced changes	Space	Latitude	0.101	0	0	0.101	0.48
		Longitude	0.238	0	0	0.238	0.10
	Climate	Temperature (PC1)	0	0	0	0	0.97
		Temperature (PC2)	**0.217**	**0**	**0.164**	**0.381**	**0.07**
		Precipitation (PC1)	0	0	0	0	0.96
		Precipitation (PC2)	0	0	0.081	0.081	0.36
	Habitat amount	**Forest cover**	**0**	**0.302**	**0.142**	**0.444**	**0.07**
		Sample size	0	0	0	0	0.97
Abundance-gradients	Space	Latitude	0	0	0	0	0.95
		Longitude	0	0	0.014	0.014	0.75
	Climate	Temperature (PC1)	0.052	0	0	0.052	0.49
		Temperature (PC2)	0	0	0	0	0.96
		Precipitation (PC1)	0	0	0.054	0.054	0.51
		Precipitation (PC2)	0.065	0	0	0.065	0.48
	Habitat amount	Forest cover	0.019	0	0	0.019	0.71
		Sample size	**0.061**	**0.492**	**0.164**	**0.717**	**<0.01**

Notes. Significant ($P < 0.05$) or marginally significant ($P < 0.1$) *P*-values for the I-splines of the predictor variables after 999 permutations are given in bold. PC1 and PC2 refer to the first two axes of the respective principal component analyses of temperature or precipitation variables (see *Methods*).

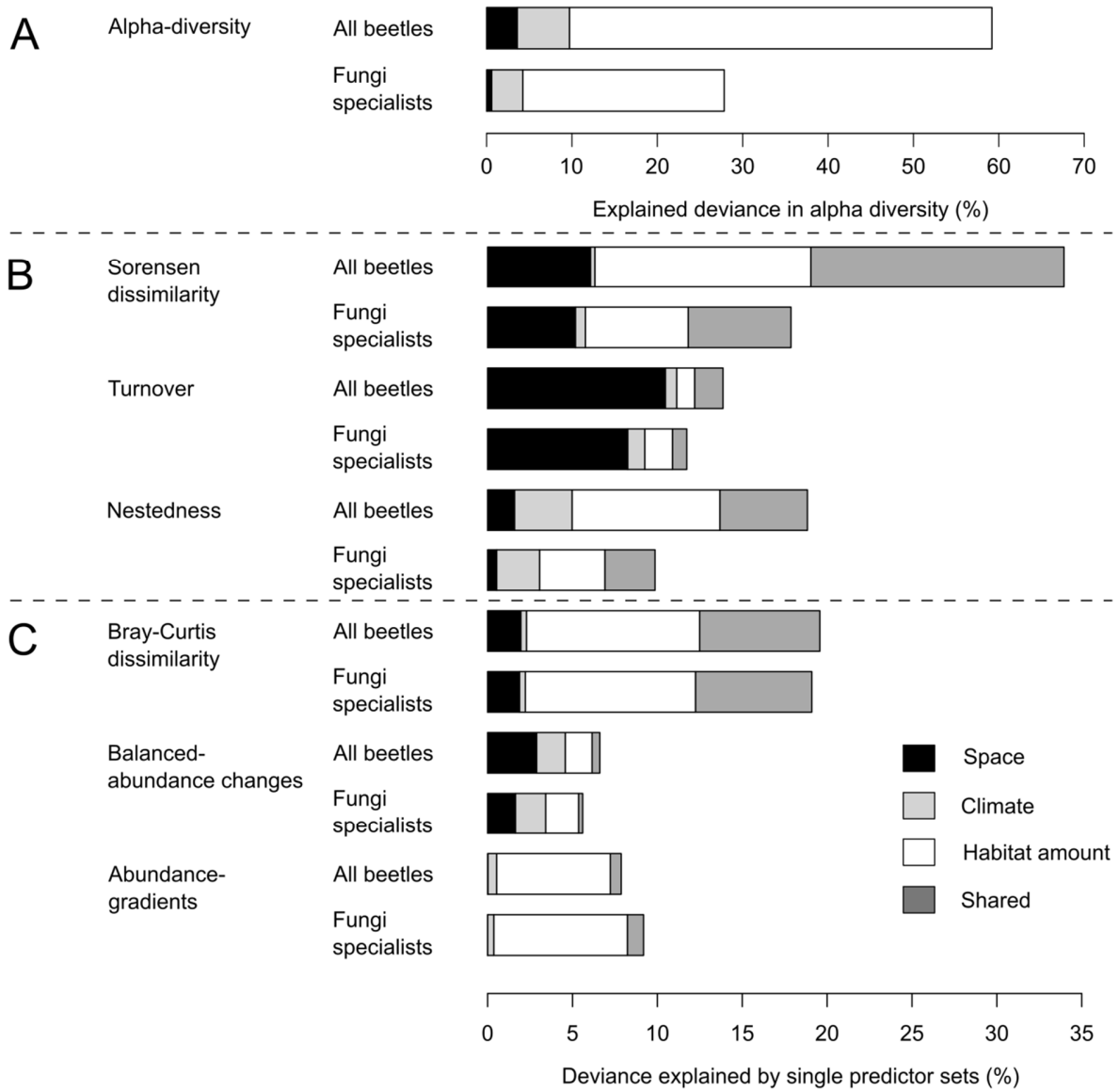

FIGURE 7.2.5. Relative contribution of predictor sets in explained deviance of (A) alpha-diversity, (B) presence-absence based beta-diversity and its components turnover and nestedness and (C) abundance-based beta-diversity and its components of balanced-abundance changes and abundance-gradients. Alpha-diversity was modelled using generalized linear models and the relative contribution is based on hierarchical partitioning. Beta-diversity based on presence absence data or abundance data and its components were modelled using generalized dissimilarity models and the relative contribution was calculated as the 'pure' effect of the predictor set on the overall explained deviance of the model. All analyses were conducted for all beetle species and fungi specialists separately. Bar colors represent the predictor sets with space in black, climate in lightgrey, habitat amount in white and the deviance shared by the predictors in darkgrey.

Chapter 8.1

Appendix chapter 3.1

Habitat availability drives the distribution-abundance relationship in phytophagous true bugs in managed grasslands

with
Martin M. Gossner | Wolfgang W. Weisser | Roland Brandl | Martin Brändle

published in Ecology, 98 (10), 2017, p. 2561 – 2573

Range-position of species

We derived occurrence data for the countries of the Palearctic from the literature (Aukema and Rieger 1995, 1996, 1999, 2001, 2006). From the occurrence information we created polygons consisting of the countries where a species was reported. From these polygons we calculated the centroids using the *gCentroid* function of the *rgeos* package (Bivand and Rundel 2016). We then calculated the distances from the centroid of a species to the three study regions separately using the *distHaversine* function from the *geosphere* package (Figure 8.1.1; Hijmans 2016). Furthermore, we calculated the area of the polygons and fitted a linear model of the distance to the centroid against the area (Figure 8.1.2). For the analyses we used the residuals from the linear model as a measure for the range position corrected for the area of the range.

Morphometric traits

We performed a principal component analysis on the covariance matrix of the $\log_e$-transformed measures to obtain uncorrelated estimates. We extracted three principal components using the *rda*-function implemented in the *vegan* package (Oksanen et al. 2015). On the first axis all variables loaded equally strong with body volume, hind femur length and wing length having positive and hind femur width negative loadings. Except for the hind femur width, which apparently is negatively correlated with hind femur length and body volume, the first axis is an integrative index for the overall body size of the species (for the loadings see Table 8.1.1). On the second axis all variables loaded positive, while the hind femur width had the highest loading values, followed by the wing size. It therefore represents a species ability to jump and fly. On the third axis hind femur length showed strong positive and body volume strong negative loadings. It represents the relative length of the femur and therefore the ability of walking.

Host plants of true bug species

Information on the host plants of the true bug species were derived from the literature (Wachmann et al. 2004, 2006, 2007, 2008, 2012). Information on whether a plant species is to be considered a primary or a secondary host plant was evaluated by whether a species is considered to feed on a plant often or mostly, or respectively infrequent or rarely. A complete list of the host plants of the species is provided in Digital Supplementary.

Extended Acknowledgments

We thank the managers of the three Biodiversity Exploratories—Swen Renner, Sonja Gockel, Kerstin Wiesner, and Martin Gorke—for their work in maintaining the sites and project infrastructure; Simone Pfeiffer and Christiane Fischer in the central office for support; Michael Owonibi for managing the central database; and Markus Fischer, Eduard Linsenmair, Dominik Hessenmöller, Jens Nieschulze, Daniel Prati, Ingo Schöning, François Buscot, Ernst-Detlef Schulze, and the late Elisabeth Kalko for their roles in setting up the Biodiversity Exploratories project. We are grateful to Esther Pašalić, Markus Lange, Manfred Türke, Luis Sikora, Ellen Sperr, and Kaspar Kremer for sweep-net sampling; Nadja Simons, Iris Gallenberger, Petra Freynhagen, and Marco Lutz for support in sample processing; Wolfgang Rabitsch for information on the European distribution of Heteroptera; and Franz Schmolke for species identification. The plant data were kindly provided by the Core project Botany of the Biodiversity

Exploratories. This work was partly funded by the DFG Priority Program 1374 "Infrastructure-Biodiversity-Exploratories" (DFG-BR 1967/9-1, DFG-WE 3081/21-1). Field work permits were issued by the responsible state environmental offices of Baden-Württemberg, Thüringen, and Brandenburg (according to § 72 BbgNatSchG).

TABLE 8.1.1. Loadings of the principal component analysis of morphometric traits. Values in brackets refer to the explained variance by the respective axis.

Predictor	PC1 (83 %)	PC2 (8 %)	PC3 (7 %)	PC4 (2 %)
Body volume	2.06	0.38	-0.81	-0.30
Hind femur length	2.08	0.03	0.83	-0.32
Hind femur width	-1.97	1.09	0.18	-0.14
Wing length	2.12	0.61	0.14	0.45

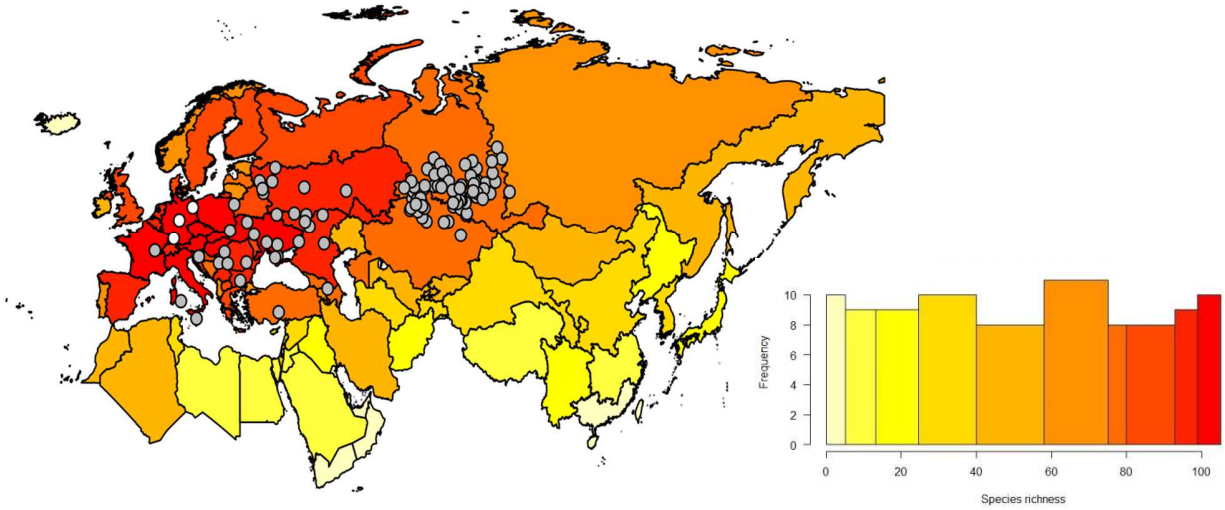

FIGURE 8.1.1. Map of the Palearctic with the centroids of the species ranges (gray circles) and the location of the three study regions (white circles). Centroids are based on polygons consisting of the countries where a species was reported, according to Aukema and Rieger (1995, 1996, 1999, 2001, 2006). Colors of the countries correspond to the number of species included in our study with reported occurrences in the respective county (see histogram).

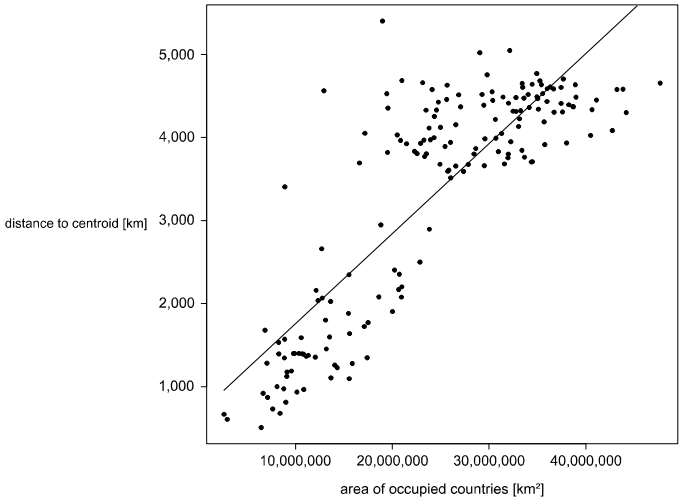

FIGURE 8.1.2. Linear relationship of the distance from the study regions to the centroid of the range of a species and the area of the occupied countries (Linear model: $r^2 = 0.71$, $P < 0.001$).

TABLE 8.1.2. Variables used in the analyses with a short description, the range, mean, standard deviation from the mean and the transformation conducted prior to the analysis.

Variable	Range	Mean	SD	Transformation	Description
Mean abundance	{0.17, 23.52}	1.62	2.86	$\log_e$	The mean of the individuals of the true bug species over the study period per study region.
Local distribution	{0.02, 1}	0.21	0.27	logit	The proportion of sites occupied by the true bug species at least once during the study period per study region
Resource occupancy $_{primary}$	{0, 1}	0.68	0.37	logit	The proportion of the sites where the primary host-plant occurred at least once during the study period per study region.
Resource occupancy $_{secondary}$	{0, 1}	0.38	0.46	logit	The proportion of the sites where the secondary host-plant occurred at least once during the study period per study region.
Resource density $_{primary}$	{0, 478.67}	34.36	77.68	$\log_e$+ 1	The mean ground cover of primary host-plants over the study period per study region.
Resource density $_{secondary}$	{0, 445.49}	26.33	74.1	$\log_e$+ 1	The mean ground cover of secondary host-plants over the study period per study region.
Body size	{-0.23, 0.23}	0.01	0.10	-	The first axis of a principal component analysis (PCA) of body volume, hind femur length, hind femur width and wing length.
Flying/jumping	{-0.30, 0.22}	0.00	0.10	-	The second axis of a principal component analysis (PCA) of body volume, hind femur length, hind femur width and wing length.
Walking	{-0.21, 0.24}	0.00	0.10	-	The third axis of a principal component analysis (PCA) of body volume, hind femur length, hind femur width and wing length.
Range-position	{-1.46E+06, 2.61E+06}	-1.35E+05	6.44E+06	-	The residuals of the linear relationship between the centroid of the Palearctic distribution of the true bug species and the area of the distribution based on country-wise presence-absence data.
Land-use intensity	{0.56, 3.06}	1.51	0.41	-	The mean Land-use intensity index of the sites where the true bug species occurred over the study period per study region.
Feeding specialization	-	-	-	-	The grade of specialization as a factor or coded as an integer with three levels: monophagous (3), oligophagous (2) and polyphagous (1).
Body volume	{1.07, 355.87}	39.68	76.11	$\log_e$	The body volume of the true bug species calculated as the product of length, width and height measured in mm.
Hind femur length	{0.42, 4.88}	2.11	0.96	$\log_e$	The hind femur length of the true bug species measured in mm.
Hind femur width	{1.34, 8.70}	3.43	1.68	$\log_e$	The hind femur width of the true bug species measured in mm.
Wing length	{1.66, 9.64}	4.56	1.88	$\log_e$	The wing length of the true bug species measured in mm.

TABLE 8.1.3. Structural equations used in the piecewise structural equation models for the analyses excluding polyphagous species.

Model and response	Structural equations	R^2_M	R^2_C	*C*	df	*P*	AIC_C	K
a								
Abundance	~range position	<0.01	0.64	136.9	2	<	158.6	10
Distribution	~range position	0.01	0.69			0.001		
b								
Abundance	~feeding specialization	0.07	0.64	131.4	2	<	153.1	10
Distribution	~feeding specialization	0.07	0.69			0.001		
c								
Abundance	~resource density$_{primary}$ + resource density$_{secondary}$	0.57	0.76	288.7	16	<	341.5	22
Distribution	~resource distribution$_{primary}$ + resource distribution$_{secondary}$	0.21	0.73			0.001		
Resource density$_{primary}$	~resource distribution$_{primary}$	0.38	0.82					
Resource density$_{secondary}$	~resource distribution$_{secondary}$	0.62	0.90					
d								
Distribution	~abundance + body size + flying/jumping ability + walking ability	0.73	0.86	-	-	-	209.4	-
e								
Abundance	~distribution + resource density$_{primary}$ + resource density$_{secondary}$ body size + flying/jumping ability + walking ability + feeding specialization	0.73	0.84	69.4	6	< 0.001	113.9	19
Distribution	~abundance + body size + flying/jumping ability + walking ability	0.73	0.86					
f								
Abundance	~distribution	0.73	0.84	4.5	4	0.35	31.0	12
Distribution	~resource density$_{primary}$ + resource density$_{secondary}$	0.84	0.92					
All								
Abundance	~distribution + body size + flying/jumping ability + walking ability + feeding specialization + resource density$_{secondary}$ + range position	0.74	0.84	0.4	2	0.81	56.1	23
Distribution	~abundance + body size + flying/jumping ability + walking ability + feeding specialization + resource density$_{primary}$ + resource density$_{secondary}$ + range position	0.85	0.92					

Notes: Model refers to the corresponding hypotheses in Fig. 3.1.1 and 3.1.2. All models included genus and species identity as a nested random factor. The related hypotheses are as follows, (a) range-position hypothesis, (b) resource-use hypothesis, (c) resource-availability hypothesis, (d) density-dependent habitat selection, (e) metapopulation dynamics, (f) habitat-dispersal hypothesis and (all) all hypotheses combined (Fig. 3.1.5). Reported statistics include marginal R^2 (R^2_M), conditional R^2 (R^2_C), Fisher's *C*, the chi-squared test degrees of freedom (df), *P*-value of the Chi-squared significance test, AIC_C value (AIC_C) and the likelihood degrees of freedom (*K*). Note that model (d) is based on a regular linear mixed effect model and thus the statistics for piecewise structural equation models are not available. The subscript 'primary' and 'secondary' refers to primary and secondary host-plants (see *Methods* in chapter 3.1).

TABLE 8.1.4. Results from the piecewise structural equation modelling for the analyses excluding polyphagous species, including standardized effect sizes (SES), standard errors (SE), *P*-values (*P*) and the variance inflation factor (VIF).

Model and response	Predictor	SES	SE	*P*	VIF
a					
Mean abundance	range-position	-0.08	0.10	0.46	1.00
Local distribution	range-position	-0.10	0.09	0.29	1.00
b					
Mean abundance	**feeding specialization**	**-0.26**	**0.10**	**< 0.05**	**1.00**
Local distribution	**feeding specialization**	**-0.24**	**0.10**	**< 0.05**	**1.00**
c					
Mean abundance	**resource density$_{primary}$**	**0.60**	**0.08**	**< 0.001**	**1.24**
Mean abundance	**resource density$_{secondary}$**	**0.27**	**0.08**	**< 0.01**	**1.24**
Local distribution	**resource distribution$_{primary}$**	**0.38**	**0.08**	**< 0.001**	**1.08**
Local distribution	resource distribution$_{secondary}$	0.12	0.09	0.24	1.08
Resource density$_{primary}$	**resource distribution$_{primary}$**	**0.54**	**0.06**	**< 0.001**	**1.00**
Resource density$_{secondary}$	**resource distribution$_{secondary}$**	**0.69**	**0.06**	**< 0.001**	**1.00**
d					
Local distribution	**mean abundance**	**0.71**	**0.06**	**< 0.001**	**1.17**
Local distribution	body size	0.09	0.06	0.12	1.04
Local distribution	flying/jumping ability	0.02	0.06	0.77	1.01
Local distribution	**walking ability**	**0.15**	**0.06**	**< 0.05**	**1.14**
e					
Mean abundance	**local distribution**	**0.79**	**0.10**	**< 0.001**	**3.57**
Mean abundance	resource density$_{primary}$	-0.01	0.10	0.92	3.41
Mean abundance	resource density$_{secondary}$	0.10	0.07	0.19	1.51
Mean abundance	feeding specialization	-0.05	0.06	0.48	1.39
Mean abundance	body size	-0.02	0.06	0.80	1.24
Mean abundance	flying/jumping ability	-0.05	0.06	0.37	1.02
Mean abundance	walking ability	-0.02	0.06	0.80	1.29
Local distribution	**mean abundance**	**0.71**	**0.05**	**< 0.001**	**1.16**
Local distribution	body size	0.09	0.06	0.13	1.04
Local distribution	flying/jumping ability	0.02	0.06	0.77	1.01
Local distribution	**walking ability**	**0.15**	**0.06**	**< 0.05**	**1.14**
f					
Mean abundance	**local distribution**	**0.86**	**0.05**	**< 0.001**	**1.00**
Local distribution	**mean abundance**	**0.44**	**0.05**	**< 0.001**	**1.83**
Local distribution	**resource density$_{primary}$**	**0.48**	**0.06**	**< 0.001**	**1.72**
Local distribution	**resource density$_{secondary}$**	**0.12**	**0.05**	**< 0.05**	**1.26**
All					
Mean abundance	**local distribution**	**0.80**	**0.07**	**< 0.001**	**1.69**
Mean abundance	range-position	0.06	0.05	0.30	1.12
Mean abundance	feeding specialization	-0.06	0.06	0.33	1.36
Mean abundance	resource density$_{secondary}$	0.10	0.07	0.15	1.52
Mean abundance	body size	-0.02	0.06	0.80	1.17
Mean abundance	flying/jumping ability	-0.05	0.06	0.38	1.03
Mean abundance	walking ability	0.05	0.06	0.47	1.31
Local distribution	**mean abundance**	**0.42**	**0.05**	**< 0.001**	**1.97**
Local distribution	range-position	-0.04	0.04	0.40	1.11
Local distribution	feeding specialization	0.08	0.05	0.12	1.41
Local distribution	**resource density$_{primary}$**	**0.51**	**0.06**	**< 0.001**	**2.05**
Local distribution	**resource density$_{secondary}$**	**0.14**	**0.05**	**< 0.05**	**1.40**
Local distribution	body size	-0.05	0.05	0.36	1.20
Local distribution	flying/jumping ability	0.01	0.04	0.40	1.02
Local distribution	walking ability	0.09	0.05	0.10	1.24

Notes. Lower case letter in the column model corresponds to the structural equations in Table 3.1.1 and the path diagrams in Figures 3.1.4 and 3.1.5 of chapter 3.1. Significant effects are in bold. The subscript 'primary' and 'secondary' refers to primary and secondary host-plants (see *Methods* in chapter 3.1).

TABLE 8.1.5. Results from the piecewise structural equation modelling for the analyses including the mean land-use intensity (LUI) as a fixed effect. We tested whether the mean LUI has a significant effect on either mean abundance or local distribution when tested alone or in the combine framework including all other variables from the main analysis. We performed the analysis once including and once excluding polyphagous species. Reported statistics include standardized effect sizes (SES), standard errors (SE), P-values (P) and the variance inflation factor (VIF). Significant effects are in bold. The subscripts 'primary' and 'secondary' refer to primary and secondary host-plants (see *Methods* in chapter 3.1).

Model and response	Predictor	SES	SE	*P*	VIF
Including polyphagous species					
Mean abundance	mean LUI	0.03	0.06	0.56	1.00
Local distribution	mean LUI	0.06	0.05	0.25	1.00
Excluding polyphagous species					
Mean abundance	mean LUI	**-0.26**	**0.10**	**< 0.05**	**1.00**
Local distribution	mean LUI	**-0.24**	**0.10**	**< 0.05**	**1.00**
Including polyphagous species					
Mean abundance	**local distribution**	**0.81**	**0.05**	**< 0.001**	**1.35**
Mean abundance	range-position	0.04	0.05	0.39	1.19
Mean abundance	feeding specialization	-0.01	0.05	0.81	1.27
Mean abundance	resource density$_{secondary}$	0.10	0.05	0.08	1.30
Mean abundance	body size	-0.01	0.05	0.98	1.20
Mean abundance	flying/jumping ability	-0.04	0.05	0.45	1.04
Mean abundance	walking ability	0.03	0.05	0.56	1.19
Mean abundance	mean LUI	-0.04	0.04	0.23	1.07
Local distribution	**mean abundance**	**0.43**	**0.05**	**< 0.001**	**1.99**
Local distribution	range-position	-0.05	0.04	0.19	1.14
Local distribution	feeding specialization	0.02	0.04	0.66	1.26
Local distribution	**resource density$_{primary}$**	**0.47**	**0.05**	**< 0.001**	**2.01**
Local distribution	**resource density$_{secondary}$**	**0.10**	**0.04**	**< 0.05**	**1.26**
Local distribution	body size	-0.06	0.05	0.23	1.23
Local distribution	flying/jumping ability	0.02	0.04	0.56	1.03
Local distribution	walking ability	0.07	0.04	0.12	1.12
Local distribution	mean LUI	0.01	0.03	0.68	1.07
Excluding polyphagous species					
Mean abundance	**local distribution**	**0.78**	**0.07**	**< 0.001**	**1.70**
Mean abundance	range-position	0.06	0.05	0.30	1.12
Mean abundance	feeding specialization	-0.09	0.06	0.18	1.46
Mean abundance	resource density$_{secondary}$	0.11	0.07	0.14	1.52
Mean abundance	body size	-0.01	0.06	0.95	1.19
Mean abundance	flying/jumping ability	-0.07	0.06	0.24	1.07
Mean abundance	walking ability	0.05	0.06	0.46	1.32
Mean abundance	mean LUI	-0.08	0.05	0.11	1.17
Local distribution	**mean abundance**	**0.42**	**0.05**	**< 0.001**	**2.00**
Local distribution	range-position	-0.04	0.04	0.38	1.11
Local distribution	feeding specialization	0.09	0.05	0.09	1.50
Local distribution	**resource density$_{primary}$**	**0.51**	**0.06**	**< 0.001**	**2.07**
Local distribution	**resource density$_{secondary}$**	**0.13**	**0.05**	**< 0.05**	**1.42**
Local distribution	body size	-0.05	0.05	0.30	1.22
Local distribution	flying/jumping ability	0.01	0.04	0.78	1.05
Local distribution	walking ability	0.09	0.05	0.09	1.25
Local distribution	mean LUI	0.03	0.04	0.35	1.16

Chapter 8.2

Appendix chapter 3.2

Mobility costs and energy uptake modulate the occurrence of butterflies

with
Stefan Pinkert | Dirk Zeuss | Martin M. Gossner | Roland Brandl | Stefan Brunzel

a modified version of this article is under review at *Nature Communitcations*

Wingbeat frequency

To quantify the energetic costs of mobility, we calculated the wingbeat frequency of butterfly individuals based on footage from a high-speed camera (300 frames/s, type RED Epic-X 5k; see Digital Supplementary for an example film clip). We analysed a total footage of 44.11 min (793,896 frames/2,646 s) of 332 individuals of 102 species (median: 3,864 frames/species; min: 480 frames/species; max: 39,684 frames/species). Wingbeats were counted independently by two people using a slow-motion playback at a rate of 25 frames/s. Wingbeat frequencies from the two counts of the same scene always differed by less than one wingbeat and were averaged. Since the species *Thymelicus sylvestris* and *Thymelicus lineola* are difficult to separate based on their phenotype, we pooled wingbeat counts for the two species and considered their wingbeat frequencies to be equal. In addition, we used published wingbeat frequencies of *Aglais io* and *Pararge aegeria* for our analysis[1,2]. Note that the intraspecific variation in wingbeat frequencies was generally low (Fig. 3.2.1). Only wingbeats of *Hesperia comma* showed large intraspecific variation. For 58 species that were recorded during normal flight (n = 59) and escape flight (n = 101), we showed that normal and peak wingbeat frequencies were strongly linearly related (estimate ± SE: 0.997 ± 0.0644, $r^2 = 0.81$, $P < 0.001$; Fig. 8.2.2). To integrate across both normal and peak wing beat frequencies of species, we therefore predicted missing based their relationship and subsequently averaged these values.

Propensity for nectar foraging

Adult butterflies are mainly generalist nectarivores[3]. To obtain a proxy for the energy uptake of adult butterflies, we therefore assumed that nectar quantity rather than nectar quality is important. In other words, species that spend more time collecting nectar during a given timespan should take up more energy than species that spend less time collecting nectar. This simplification is reasonable as sugar concentrations of flowers visited by butterflies are similar because of two important constraints. First, the sweetest nectar offers the highest reward for pollinators. Thus, competition between co-occurring flowering plants maximises the sugar concentration of their nectar[4]. Second, as an increase in sugar concentrations is associated with an increase in viscosity, the upper limit of the sugar concentration of flowers is defined by the 'foraging' technique of their pollinators, which is active sucking in the case of butterflies[5].

Following an approach that has been successfully applied to extract data on geographical variation in phenotypic trait[6], we therefore counted how often individuals were observed collecting nectar from flowers based on the results of a Google Images search (accessed on May 15, 2017). Of the first 100 hits, only images of clearly identifiable and living adult individuals were selected for further analyses (median = 57.5, min = 41, max = 77). We assigned each image a value of 1 or 0 depending on whether individuals were observed foraging or not or a value of 0.5 if they sat on a flower but the proboscis was not visible. Subsequently, these values were averaged for each species.

We used the international homepage (i.e. google.com) and searched for the scientific name of butterfly species to avoid potential bias of the access point that might result from Google's search algorithms. The propensity for nectar foraging (proportion of images showing individuals collecting nectar) showed a right-skewed distribution with values ranging from 0 to 0.59 (Fig. 8.2.7). In addition to this image-based estimation, we asked six experts on European butterflies to classify the nectar-

foraging propensity of species based on their experience in the field (levelled classes: 1 = no foraging or unusual occurrence, 2 = rarely forage, 3 = average foraging, 4 = forage often, 5 = forage very often). Finally, these classifications were standardised (z-scaled) and pooled. Spearman rank correlations indicated that estimates of the nectar-foraging propensity of a species based on images and expert classifications were strongly positively correlated ($P < 0.001$, rho = 0.31, n = 436; see also Fig. 8.2.4).

The propensity for nectar foraging (proportion of images showing individuals collecting nectar) showed a right-skewed distribution with values ranging from 0 to 0.59 (Fig. 8.2.7). In addition to this image-based estimation, we asked six experts on European butterflies to classify the nectar-foraging propensity of species based on their experience in the field (levelled classes: 1 = no foraging or unusual occurrence, 2 = rarely forage, 3 = average foraging, 4 = forage often, 5 = forage very often). Finally, these classifications were standardised (z-scaled) and pooled. Spearman rank correlations indicated that estimates of the nectar-foraging propensity of a species based on images and expert classifications were strongly positively correlated ($P < 0.001$, rho = 0.31, n = 436; see also Fig. 8.2.4).

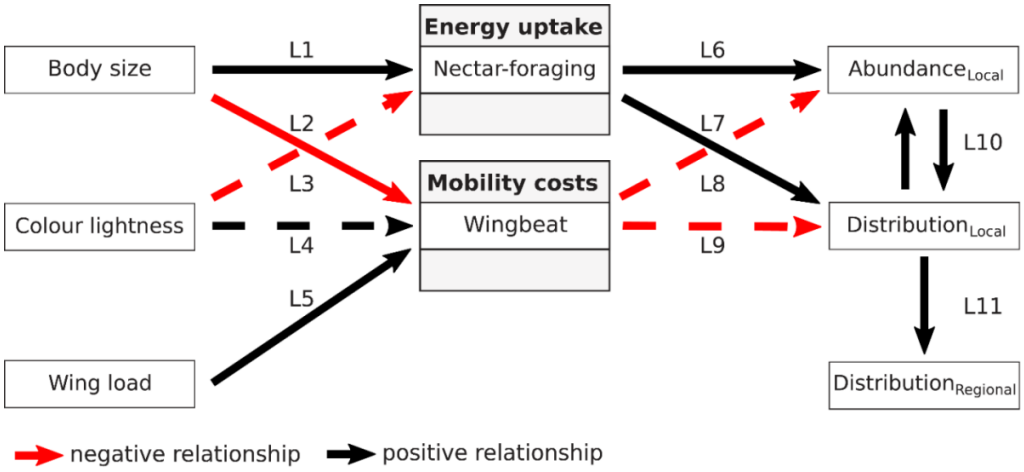

FIGURE 8.2.1. Predicted effects of morphological traits of species on their distribution and abundance via proxies for mobility costs and energy uptake. Arrows indicate the direction of putative causality as currently supported (solid lines) or hypothesised in the text (dashed lines). Specifically, we hypothesised that species compensate for the costs of morphological traits by reducing mobility costs (L2, L3, L5) or increasing energy uptake (L1, L4) or both. A successful compensation should have a positive effect on species distribution and/or abundance (L6, L7, L8, L9). Two arrows with opposing direction indicate unresolved causal relationships (L10). Examples for supported links are: L1: Tiple et al. 2009 L2: Corben 1983, L5: Betts and Wootton 1988, L6: Boggs and Freeman 2005, L7: Stevens et al. 2012, L10: Friess et al. 2017, L11: Brändle and Brandl 2001b.

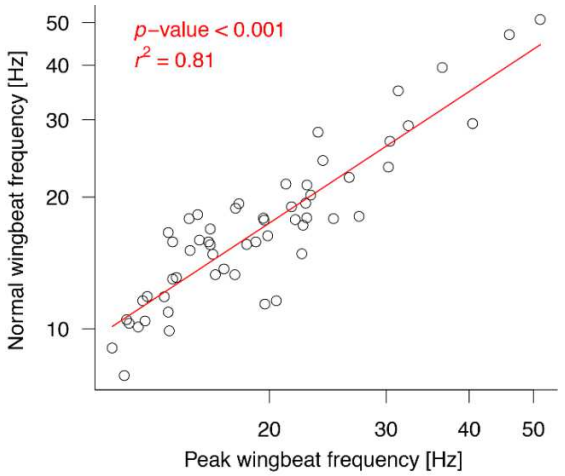

FIGURE 8.2.2. Linear regression between normal and peak wingbeat frequencies of 58 European butterfly species. The similar scale and strong correlation of the two frequencies indicate that they are directly comparable.

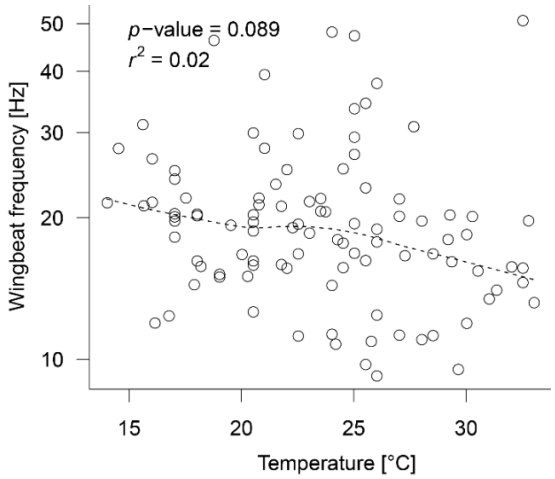

FIGURE 8.2.3. Spline-based smoothed regression of the relationship between average wingbeat frequency of 102 European butterfly species and ambient temperature during flight.

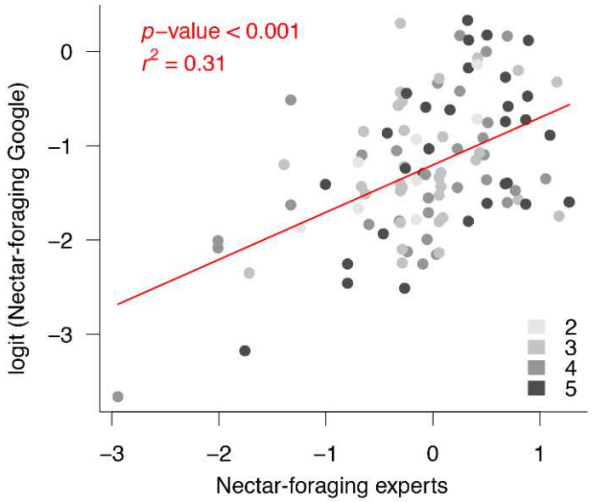

FIGURE 8.2.4. Weighted linear regression between estimates of nectar-foraging propensity based on images and expert classifications of 102 European butterfly species. The expert-based estimate of nectar-foraging propensity of species (five levelled classes) represents the average of standardized (z-scaled) expert classifications. Point colors indicate the number of available opinions (i.e. the weight) for each species.

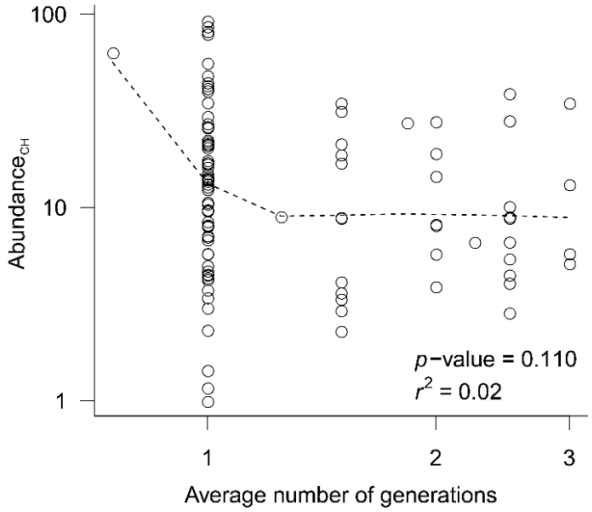

FIGURE 8.2.5. Spline-based smoothed regression of the relationship between local abundance and the average number of generations (voltinism) of 102 European butterfly species. Voltinism data was taken from Settele et al. (2000). Multiple values and ranges for species were averaged. Missing voltinism information was completed with data from Tolman and Lewington (2008).

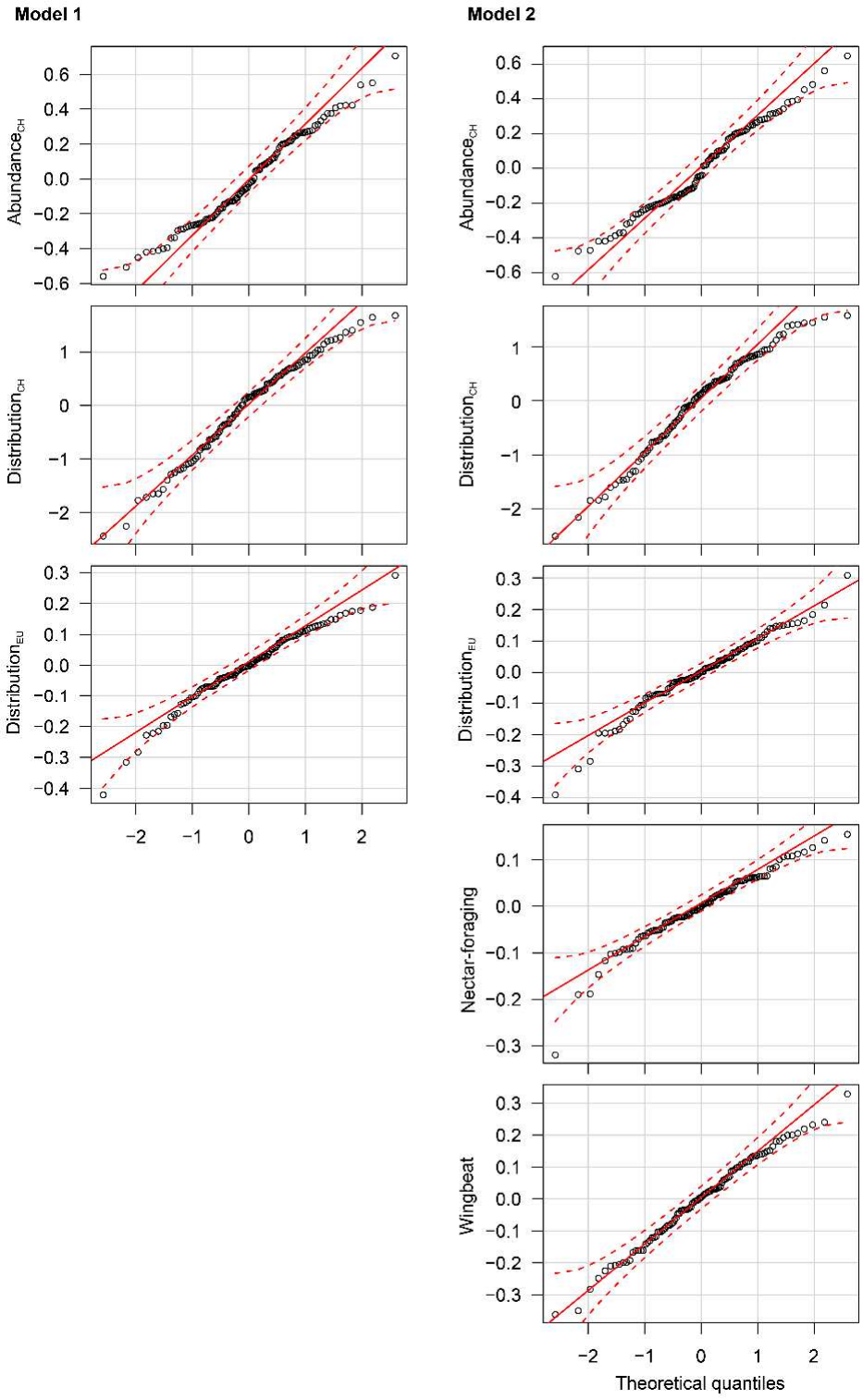

FIGURE 8.2.6. Comparison between theoretical (normal) and actual distribution of the residuals (i.e. quantile-quantile plots) of structural equations from piecewise structural equation models (for models, see Fig. 3.2.2). The subscripts CH and EU refer to variables calculated for Switzerland and Europe, respectively.

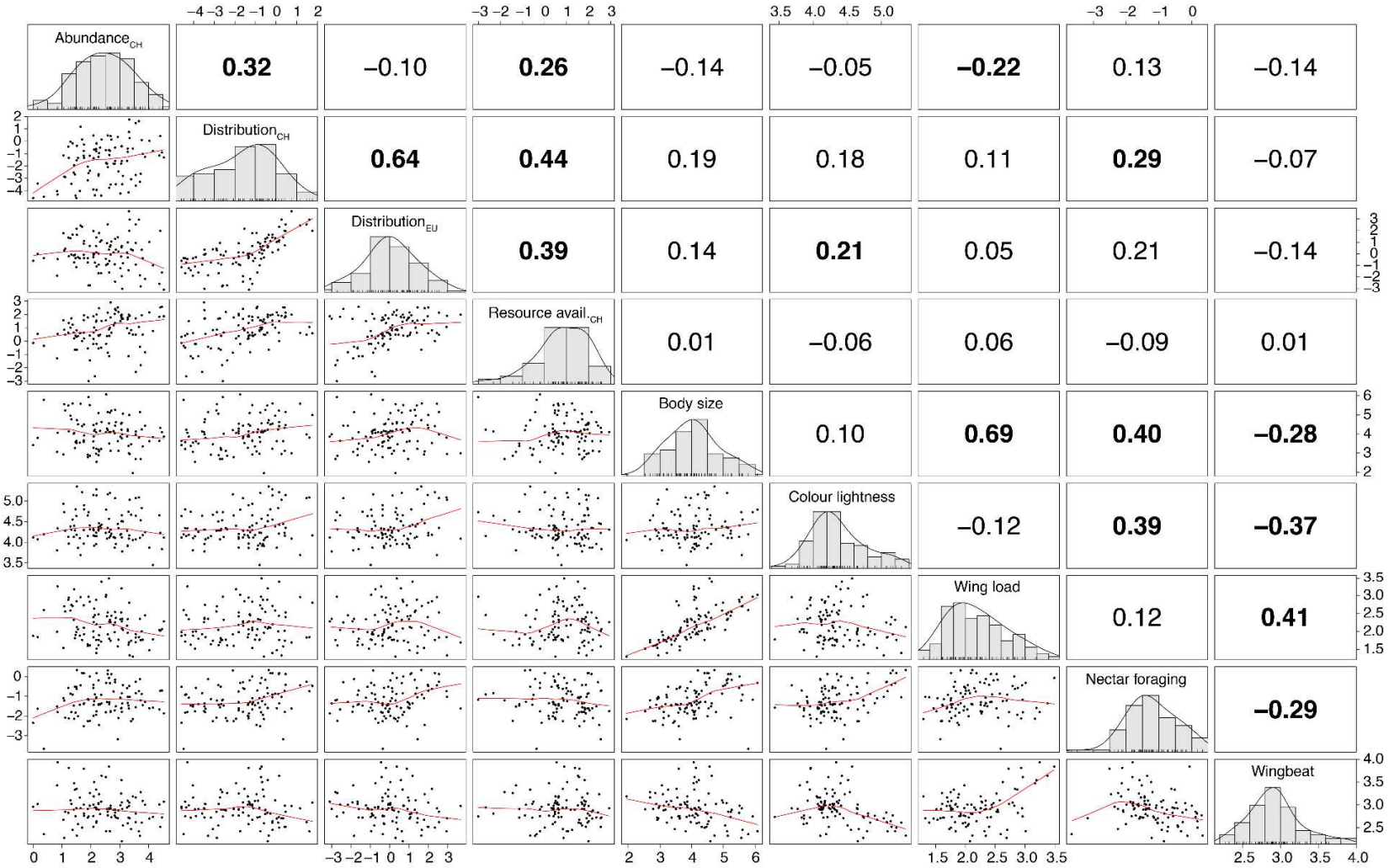

FIGURE 8.2.7. Pairwise correlations between all variables used in structural equation models. The graphs in the lower left triangle show scatterplots with spline-based smoothed regression lines. The values in the upper triangle show Pearson correlation coefficients of these correlations. Histograms in the diagonal of the matrix indicate frequency distributions of transformed variables. Significant correlations ($p < 0.05$) are in bold.

TABLE 8.2.1. Stepwise selection and variance inflation factors of predictors of structural equation models.

Model and response	Predictor	Step	VIF	
Model 1				
$Abundance_{CH}$	$Distribution_{CH}$		*	1.57
$Abundance_{CH}$	$Distribution_{EU}$	+	I	1.57
$Abundance_{CH}$	Body size	–	VII	
$Abundance_{CH}$	Wing load	–	VI	
$Abundance_{CH}$	Color lightness	–	VIII	
$Distribution_{CH}$	$Abundance_{CH}$		*	1.04
$Distribution_{CH}$	Habitat $availability_{CH}$		*	1.04
$Distribution_{CH}$	Body size	–	III	
$Distribution_{CH}$	Wing load	–	V	
$Distribution_{CH}$	Color lightness	–	IV	
$Distribution_{EU}$	$Distribution_{CH}$		*	1.24
$Distribution_{EU}$	Habitat $availability_{CH}$	+	II	1.24
Model 2				
$Abundance_{CH}$	$Distribution_{CH}$		*	1.61
$Abundance_{CH}$	$Distribution_{EU}$	+	I	1.58
$Abundance_{CH}$	Body size	+	II	1.16
$Abundance_{CH}$	Nectar-foraging		*	1.21
$Abundance_{CH}$	Wingbeat	–	VI	
$Distribution_{CH}$	$Abundance_{CH}$		*	1.11
$Distribution_{CH}$	Habitat $availability_{CH}$		*	1.07
$Distribution_{CH}$	Nectar-foraging		*	1.08
$Distribution_{CH}$	Wingbeat	–	IV	
$Distribution_{EU}$	$Distribution_{CH}$		*	1.00
$Distribution_{EU}$	Nectar-foraging	–	V	
$Distribution_{EU}$	Wingbeat	+	III	1.00
Nectar-foraging	Body size		*	1.01
Nectar-foraging	Color lightness		*	1.01
Wingbeat	Body size		*	1.92
Wingbeat	Wing load		*	1.93
Wingbeat	Color lightness		*	1.04

Notes. Stepwise predictor selection based on Chi-squared significance test and associated statistics from directed separation tests (see *Methods* in Chapter 3.2). Models correspond to the path diagrams in Figure 3.2.2. Roman numerals indicate the step at which the respective predictor variable was excluded (–) or a missing path (predictor) was included (+) into the model. The subscripts CH and EU refer to variables calculated for Switzerland and Europe, respectively. * = significant.

Chapter 9.1

Appendix chapter 4.1

The dark side of Lepidoptera: Color lightness of geometrid moths decreases with increasing latitude

with
Lea Heidrich | Konrad Fiedler | Martin Brändle | Axel Hausmann | Roland Brandl | Dirk Zeuss |

published in Global Ecology and Biogeography, 27 (4), 2018, p. 407 – 416

Data sources

Distribution and color lightness

Hausmann, A. (2001). *Introduction, Archiearinae, Orthostixinae, Desmobathrinae, Alsophilinae, Geometrinae*. In A. Hausmann (Ed.), The geometrid moths of Europe 1. Stenstrup, Denmark: Apollo Books.

Hausmann, A. (2004). *Sterrhinae*. In A. Hausmann (Ed.), The geometrid moths of Europe 2. Stenstrup, Denmark: Apollo Books.

Hausmann, A., & Viidalepp, J. (2012). *Larentiinae I*. In A. Hausmann (Ed.), The geometrid moths of Europe 3. Stenstrup, Denmark: Apollo Books.

Hausmann, A., Mironov, V., Sihoven, P., Skou, P., & Viidalepp, J. (2014). *The Geometrid moths of Europe (update)*. Retrieved from http://www.zsm.mwn.de/lep/gme.htm

Mironov, V. (2003). *Larentiinae II (Perizomini and Eupitheciini)*. In A. Hausmann (Ed.), The geometrid moths of Europe 4. Stenstrup, Denmark: Apollo Books.

Classification of activity patterns

Ebert, G. (Ed.) (2001). Die Schmetterlinge Baden-Württembergs, Band 8, Nachtfalter VI. Stuttgart, Germany: Verlag Eugen Ulmer.

Ebert, G. (Ed.) (2003). Die Schmetterlinge Baden-Württembergs Band 9 - Nachtfalter VII. Stuttgart, Germany: Verlag Eugen Ulmer.

Riley, A. M. (2003). British and Irish pug moths – A guide to their identification and biology. Colchester, U.K.: Harley Books.

Skou, P. (1984). Nordens Målere: Håndbog over de Danske og Fennoskandiske Arter af Drepanidae og Geometridae. Copenhagen, Denmark: Fauna Boger.

Zahm, N. (2012). Die Macrolepidoptera der Majella (Abruzzen, Italien) Teil 2: Drepanidae und Geometridae (Lepidoptera). *Fragmenta Entomologica*, 44, 169–265.

Proportion of diurnal and nocturnal species

Naturally, day length increases with latitude, and accordingly, the scope for nocturnal activity decreases during the main vegetation period. Hence, the proportion of nocturnal species within the assemblages decreases with latitude, whereas the proportion of diurnal species within the assemblages increases with latitude (Table 9.1.1). While these interspecific shifts in activity cannot explain why the color lightness within assemblages of nocturnal moths resemble the pattern predicted by the Thermal Melanism Hypothesis, *intraspecific* shifts in activity period along latitude might have led to biased results. However, this would not explain the dark coloration of assemblages of nocturnal geometrid moth in mountainous regions further south (Fig. 4.1.2a within main text), where the proportion of nocturnal and diurnal species stays constant (Table 9.1.1). Note, that diurnal and nocturnal species did not differ in their color lightness (Welch two-sample t-test, P = 0.16, Fig. 9.1.1).

Male and female color lightness

We compared color lightness of female and male geometrid moths. High values indicate light-colored species, and low values indicate dark-colored species. The color lightness of males and females did not significant differ (t-test, P = 0.66). r^2 and P-value are from an ordinary linear regression. The color lightness values of the two sexes were highly correlated (P < 0.001, r^2 = 0.91). The slope of the linear regression differed slightly from a slope of 1 (estimate = −0.04, P = 0.003), and the intercept differed slightly from 0 (estimate = 0.03, P = 0.002). Note, however, that within the data range, the bisectrix (dashed, grey line) is fully covered by the regression. Therefore, we assume that there are no biological meaningful differences between the color lightness of males and the color lightness of females.

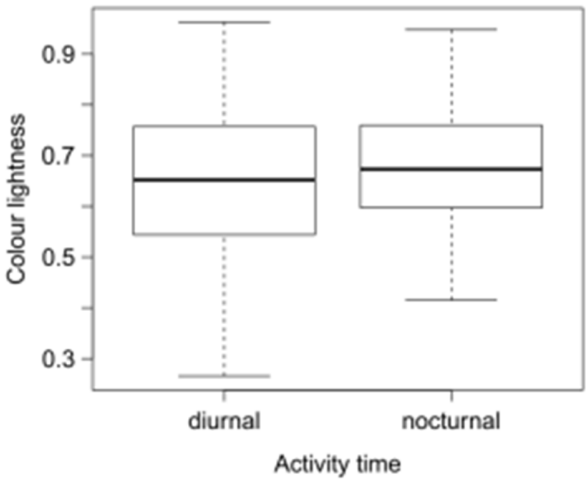

FIGURE 9.1.1. Mean color lightness of diurnal (n = 109) and nocturnal (n = 160) species. Color lightness ranging from 0 (black) to 1 (white).

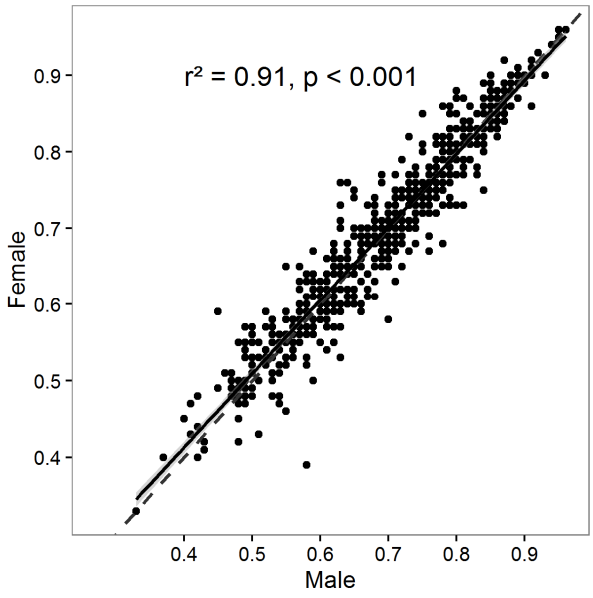

FIGURE 9.1.2. Linear regression of female to male color lightness.

TABLE 9.1.1. Results of a generalized linear model with binomial distribution and the proportion of diurnal and nocturnal species within the moth assemblages as dependent variable. ΔAIC values are the difference between the models to the intercept model.

Diel activity	Δ AIC	Variable	Estimate	±SE	z-value	*P*-value
Diurnal	-141.3	Latitude	3.68E-02	4.42E-03	8.32	<0.001
		Elevation	-3.21E-05	1.29E-04	-0.25	0.803
Nocturnal	-121.7	Latitude	-3.16E-02	3.97E-03	-7.96	<0.001
		Elevation	1.52E-05	1.08E-04	0.14	0.888

Environmental variables

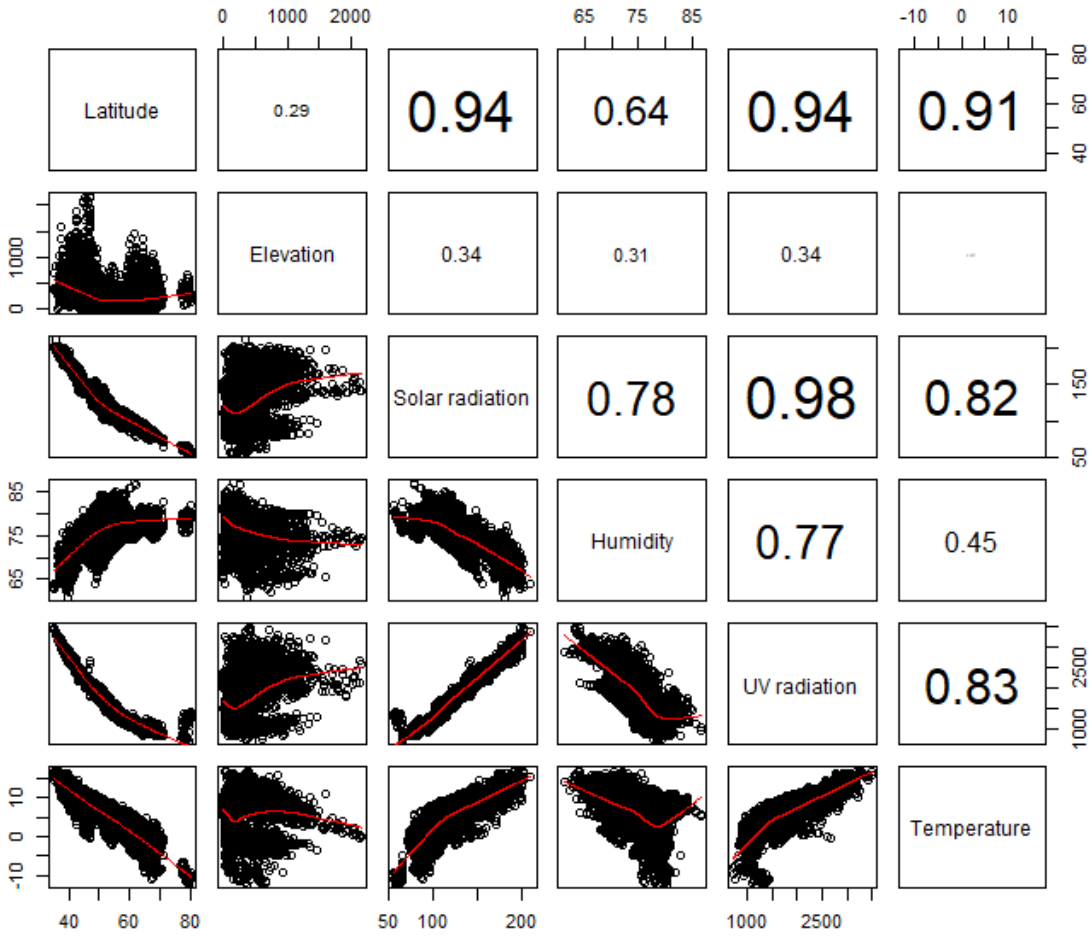

FIGURE 9.1.3. Scatterplot matrix of the used environmental variables within the generalized least square models and within the structure equation model, with Pearson R^2 indices in the right half.

Moran's I

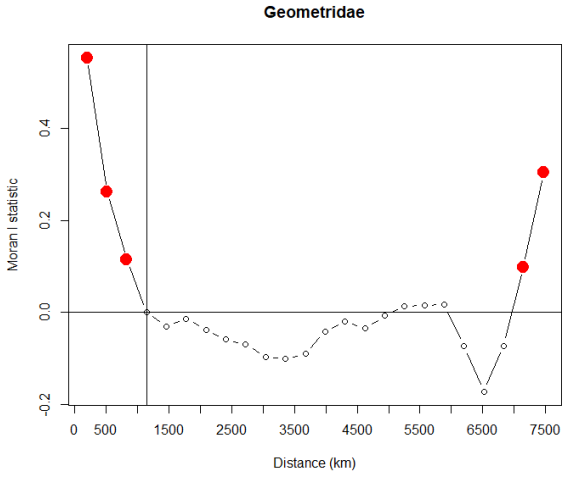

FIGURE 9.1.4. Spatial autocorrelation (Moran's I correlation coefficient) of the residuals from the model of average color lightness of 3,777 geometrid assemblages and solar radiation, humidity and the interaction thereof, weighted by the number of species. Note the spatial autocorrelation up to about a distance of 1,150 km.

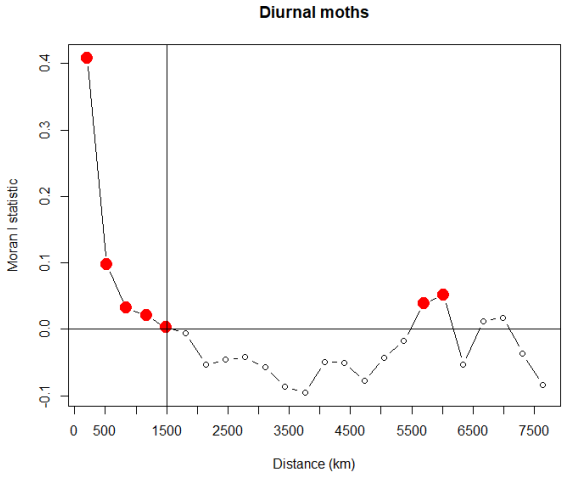

FIGURE 9.1.5. Spatial autocorrelation (Moran's I correlation coefficient) of the residuals from the model of average color lightness of 3,775 diurnal moth assemblages and solar radiation, humidity and the interaction thereof, weighted by the number of species. Note the spatial autocorrelation up to about a distance of 1,500 km.

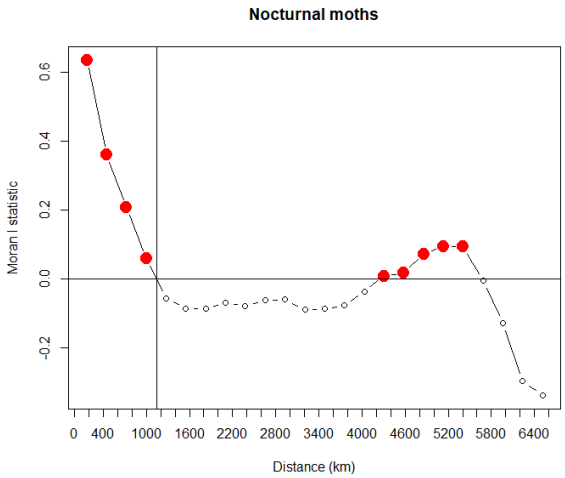

FIGURE 9.1.6. Spatial autocorrelation (Moran's I correlation coefficient) of the residuals from the model of average color lightness of 3,775 nocturnal moth assemblages and solar radiation, humidity and the interaction thereof, weighted by the number of species. Note the spatial autocorrelation up to about a distance of 1,150 km.

Null model analysis

A null model analysis was run to test whether the observed geographical variation in the color lightness of assemblages is a random effect of the proximity of the ranges of species We randomly re-sampled the color- lightness values per species but retained the species original spatial distributions, and subsequently calculated the average color lightness for each grid cell using the randomized data. This procedure was repeated 1,000 times, and the results were averaged for each grid cell. To quantify the deviation of the observed color lightness per grid (CL_{obs}) from random color- lightness values (CL_{null}), standardized effect sizes (SES) were calculated. The SES per grid cell was calculated as $(CL_{obs} - CL_{null})/sd(CL_{null})$. SES indicate significant divergence from random color lightness when the SES is larger than 1.96 or smaller than −1.96; this corresponds to the 95% confidence interval of a Gaussian distribution. For the sake of simplicity, we set the boundaries to larger than 2 or smaller than -2. Subsequently, the statistical analyses described within the method section of the main text were repeated with SES as a dependent variable for all data sets. Note, that a significant effect of the predictor variable on the color lightness of the assemblages was only considered as robust, if it occurred in the models with color lightness as well as the models with SES as dependent variable. More than 68% of the geometrid moth assemblages had significant divergence from random color lightness. In the nocturnal subset, 52% of the assemblages had significant divergence from random color lightness. In contrast, hardly more than 5% of the grid cells of the diurnal subset showed significant divergence from random color lightness. The results of the models with SES as dependent variable resemble those of the models with CL as dependent variables in large parts (see Table 9.1.2 and Table 4.1.2 within the main text). Diverging values in terms of changing variable importance or in terms of changing significance are presented in bold.

TABLE 9.1.2. Results of environmental models with SES as dependent variable. Estimated coefficients of the ordinary least squares models (OLS), weighted by the number of species per grid cell, and spatial simultaneous autoregressive models (SAR). R^2 - values of the SAR models are based on Nagelkerke. For each SAR, implemented distances were estimated with spatial correlograms (for Geometridae: 1150 km, diurnal species: 1500 km, nocturnal species: 1150 km).

	Model	Variable	Estimate	±SE	z-value	P-value	AIC	R^2
Geometridae	OLS	Radiation	9.45E-01	4.37E-02	*21.6*	< 0.001		
		Humidity	-1.09E+00	4.36E-02	*-25.1*	< 0.001	14078	0.66
		Radiation:Humidity	1.15E-01	2.51E-02	4.60	< 0.001		
	SAR	Radiation	1.84E+00	7.37E-02	25.0	< 0.001		
		Humidity	-3.89E-01	5.04E-02	-7.72	< 0.001	13168	0.64
		Radiation:Humidity	-4.17E-02	2.81E-02	-1.48	0.138		
Diurnal	OLS	Radiation	6.23E-01	2.44E-02	25.5	< 0.001		
		Humidity	-2.30E-01	2.43E-02	-9.49	< 0.001	9725	0.47
		Radiation:Humidity	1.74E-01	1.61E-02	10.8	< 0.001		
	SAR	Radiation	7.78E-01	4.12E-02	18.9	< 0.001		
		Humidity	-4.96E-02	2.79E-02	-1.78	0.075	9220	0.39
		Radiation:Humidity	5.70E-02	1.69E-02	3.37	*< 0.001*		
Nocturnal	OLS	Radiation	1.11E+00	3.80E-02	29.2	< 0.001		
		Humidity	-1.11E+00	3.79E-02	-29.3	< 0.001	12379	0.64
		Radiation:Humidity	4.75E-01	2.21E-02	21.5	< 0.001		
	SAR	Radiation	1.33E+00	6.26E-02	21.3	< 0.001		
		Humidity	-7.85E-01	4.53E-02	-17.4	< 0.001	11730	0.66
		Radiation:Humidity	2.93E-01	2.49E-02	11.8	< 0.001		

Monophyletic subfamilies

Changes in the phylogenetic composition of moth faunas also might have contributed to the continental pattern of color lightness in geometrid moths. The Larentiinae subgroup comprised 401 species, from which 169 species could be classified into nocturnal (114) were and diurnal (55) species, covering 3,776 grid cells, and the Sterrhinae subgroup 198 species, from which 74 species could be classified into nocturnal (30) and diurnal (44) species, covering 3,275 grid cells. Species belonging to the subfamily Larentiinae are on average more darkly colored (mean 0.63 ± 0.09 SD) than species belonging to the subfamily Sterrhinae (mean 0.80 ±0.09 SD; Welch two-sample t-test, t = −22.7, df'= 402, $P < 0.001$, Fig, S6.7). The decreasing share of light-colored Sterrhinae moths and the increasing share of dark-colored Larentiinae moths with latitude and elevation (Table S6.3) could thus also contribute to the observed overall gradient in color lightness. Therefore, we repeated the analysis described in the methods part to evaluate, whether the environmental variables have the same effect across these monophyletic groups.

Assemblages of Larentiinae were more darkly colored (mean 0.62 ± 0.01 SD), than assemblages of Sterrhinae (mean 0.8 ± 0.02 SD; paired t-test: t = −420, df = 3274, $P < 0.001$).

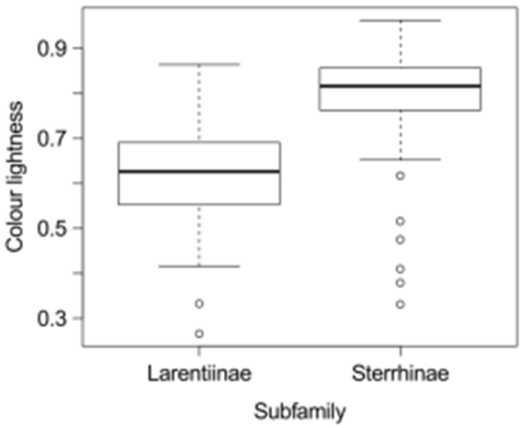

FIGURE 9.1.7. Mean color lightness of Larentiinae (n = 401) and Sterrhinae (n = 198) species. Color lightness ranging from 0 (black) to 1 (white).

TABLE 9.1.3. Results of a generalized linear model with binomial distribution and the proportion of Larentiinae and Sterrhinae species within the moth assemblages as dependent variable. ΔAIC values are the difference between the models to the intercept model.

Subtaxa	ΔAIC	Variable	Estimate	±SE	z-value	*P*-value
Larentiinae	-326.6	Latitude	5.73E-02	4.68E-03	12.2	<0.001
		Elevation	5.33E-04	1.27E-04	4.21	<0.001
Sterrhinae	-204.1	Latitude	-6.95E-02	5.33E-03	-13.0	<0.001
		Elevation	-6.66E-04	1.43E-04	-4.65	<0.001

The color lightness of Larentiinae assemblages decreased with latitude and elevation (Table S6.4; Fig. S6.8 a), whereas the color lightness of Sterrhinae increased with latitude and elevation. Note, however, that the spatial variables explained nearly nothing of the variance of the color lightness of the Sterrhinae assemblages (R^2 = 0.02, Table S6.4), which showed a more random distribution across the Western Palearctic (Fig. S6.8 b). The color lightness of assemblages of Larentiinae species increased with solar radiation and decreased with humidity both within the OLS model as well as within the SAR model. The interaction term of solar radiation and humidity had no significant effect.

After applying the SAR model, however, the interaction term gained more importance, and the positive effect of solar radiation became weaker on high levels of humidity (Table 9.1.5). In both models, the color lightness of assemblages of Sterrhinae species increased with increasing solar radiation. In contrast to the previous subsets, however, not solar radiation but humidity was the most important variable. Color lightness increased with increasing humidity. The interaction term was negative, i.e. the positive effect of solar radiation became weaker on high levels of humidity. Although the relative importance of the single variables changes between monophyletic subgroups, neither the direction nor the significance of the effects of solar radiation and humidity on color lightness changed, suggesting that the color lightness patterns are more than mere structural shifts in the faunal composition. The dominance of Larentiinae in northern Europe and the Alps (a phenomenon also recurring in other mountain areas of the world: Brehm and Fiedler, 2004) might occur precisely because of a selective advantage that is related to their darker coloration. Unfortunately, an analysis of the third large subfamily of Geometridae in Europe, namely the Ennominae, is currently precluded since the complete monograph volumes covering this subfamily that are needed to fully compare the results are not yet available.

The SES of the Sterrhinae assemblages were within values expected from random distribution, whereas 11% of the SES of the Larentiinae assemblages were higher than 2 or lower than -2. SES decreased with altitude.

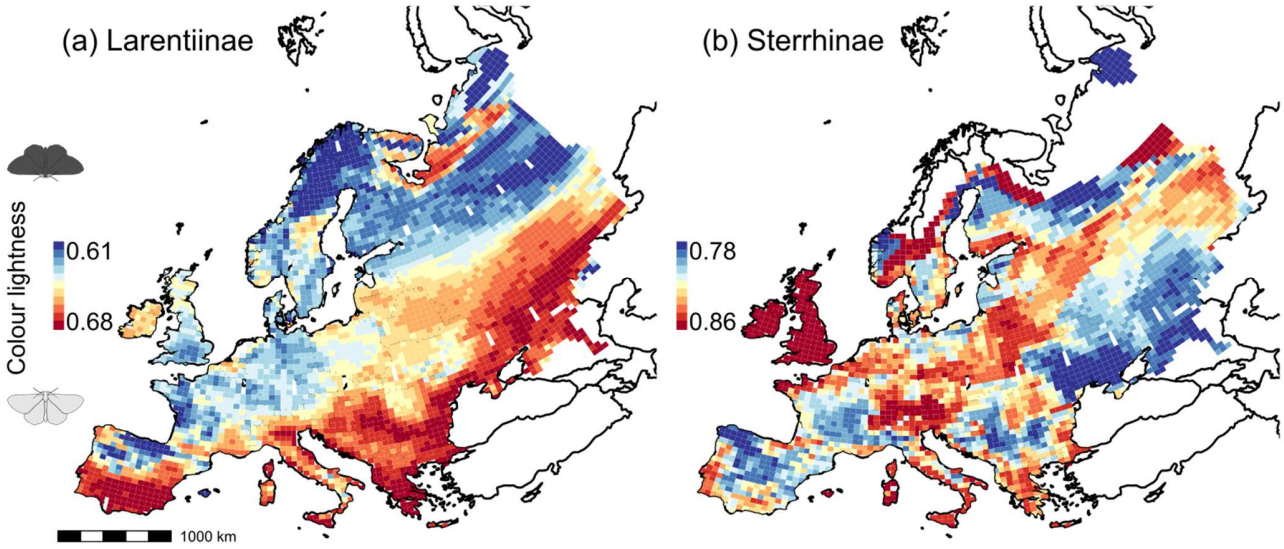

FIGURE 9.1.8. Mean color lightness of subsets of assemblages of geometrid moths across the Western Palearctic. **a)** Larentiinae (401 species, 3,776 grid cells) and **b)** Sterrhinae (198 species, 3,275 grid cells). The color coding represents quantiles ranging from 0 (black) to 1 (white), with blue indicating dark coloration and red indicating light coloration (Lambert azimuthal equal-area projection). For the subfamily Larentiinae, dark-colored species predominantly occur in northern regions and light-colored species predominantly occur in southern regions whereas the mean color lightness of assemblages of Sterrhinae shows no clear gradient.

TABLE 9.1.4. Results of spatial models. Simple linear regression with color lightness of moth assemblages as dependent and latitude and elevation as independent variables.

	Intercept	Latitude	Elevation	R^2
Larentiinae	0.686 ± 0.001	-1.10E-03 ± 2.13E-05 ***	-9.04E-06 ± 5.54E-07 ***	0.42
Sterrhinae	0.780 ± 0.003	8.55E-06 ± 4.76E-05 ***	8.55E-06 ± 1.03E-06 ***	0.02

TABLE9.1.5. Results of environmental models. Estimated coefficients of the ordinary least squares models (OLS), weighted by the number of species per grid cell, and spatial simultaneous autoregressive models (SAR). R^2- values of the SAR models are based on Nagelkerke. For each SAR, implemented distances were estimated with spatial correlograms (for Larentiinae. 1300 km, Sterrhinae: 800 km).

	Model	Variable	Estimate	±SE	*z*-value	*P*-value	AIC	R^2
Larentiinae	OLS	Radiation	0.0049	0.0003	19.1	< 0.001		
		Humidity	-0.0034	0.0003	-13.5	< 0.001	-24727	0.42
		Radiation:Humidity	0.0000	0.0002	0.15	0.882		
	SAR	Radiation	0.0059	0.0004	14.6	< 0.001		
		Humidity	-0.0012	0.0003	-4.40	< 0.001	-25941	0.64
		Radiation:Humidity	-0.0022	0.0002	-14.6	< 0.001		
Sterrhinae	OLS	Radiation	0.0027	0.0004	7.25	< 0.001		
		Humidity	0.0078	0.0004	20.7	< 0.001	-19091	0.11
		Radiation:Humidity	-0.0021	0.0002	-10.5	< 0.001		
	SAR	Radiation	0.0028	0.0007	4.25	< 0.001	-20036	0.58
		Humidity	0.0059	0.0005	11.2	< 0.001		
		Radiation:Humidity	-0.0021	0.0003	-7.28	< 0.001		

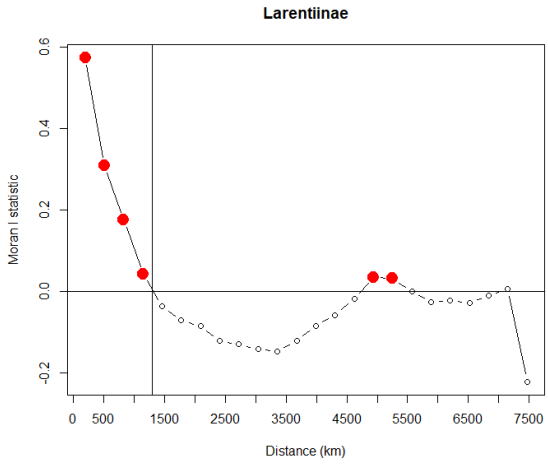

FIGURE 9.1.9. Spatial autocorrelation (Moran's I correlation coefficient) of the residuals from the model of average color lightness of 3,776 assemblages of Larentiinae and solar radiation, humidity and the interaction thereof, weighted by the number of species. Note the spatial autocorrelation up to about a distance of 1,300 km.

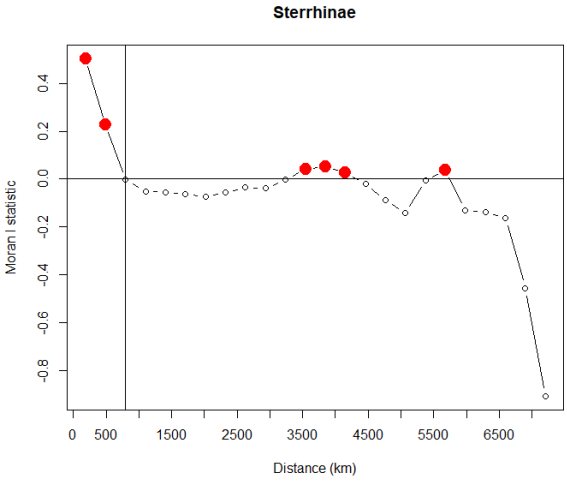

FIGURE 9.1.10. Spatial autocorrelation (Moran's I correlation coefficient) of the residuals from the model of average color lightness of 3,275 assemblages of Sterrhinae and solar radiation, humidity and the interaction thereof, weighted by the number of species. Note the spatial autocorrelation up to about a distance of 800 km.

TABLE 9.1.6. Results of environmental models with SES as dependent variable. Estimated coefficients of the ordinary least squares models (OLS), weighted by the number of species per grid cell, and spatial simultaneous autoregressive models (SAR). R^2 - values of the SAR models are based on Nagelkerke. For each SAR, implemented distances were estimated with spatial correlograms (for Larentiina 1300 km, Sterrhinae 800 km).

	Model	Variable	Estimate	SE	z-value	p-value	AIC	R^2
Larentiinae	OLS	Radiation	4.41E-01	3.08E-02	14.3	< 0.001	11405	0.41
		Humidity	-5.14E-01	3.07E-02	*-16.7*	< 0.001		
		Radiation:Humidity	4.14E-02	1.83E-02	2.26	*0.024*		
	SAR	Radiation	6.34E-01	5.05E-02	12.6	< 0.001	10523	0.47
		Humidity	-2.65E-01	3.36E-02	-7.87	< 0.001		
		Radiation:Humidity	-1.82E-01	1.91E-02	-9.53	< 0.001		
Sterrhinae	OLS	Radiation	1.28E-01	2.17E-02	5.91	< 0.001	7528	0.10
		Humidity	4.91E-01	2.21E-02	22.2	< 0.001		
		Radiation:Humidity	-1.57E-01	1.20E-02	-13.1	< 0.001		
	SAR	Radiation	2.09E-01	4.03E-02	5.18	< 0.001	6865	0.36
		Humidity	4.17E-01	3.20E-02	13.0	< 0.001		

Radiation:Humidity	-1.50E-01	1.74E-02	-8.60	< 0.001

Color lightness histograms

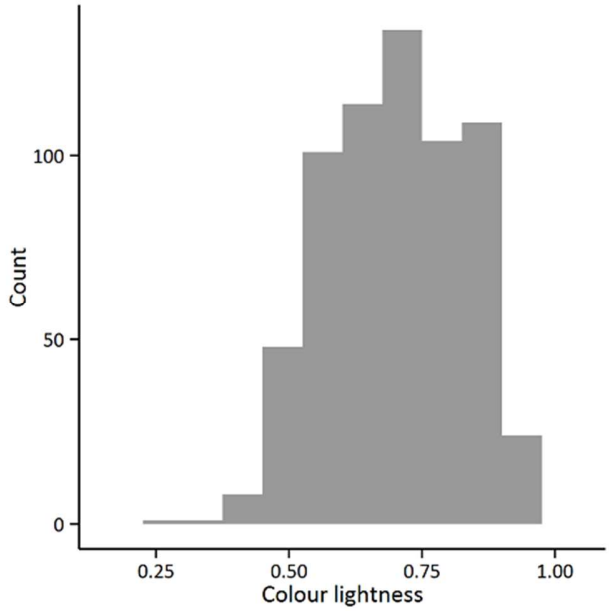

FIGURE 9.1.11. Histogram of the color lightness of geometrid moth species.

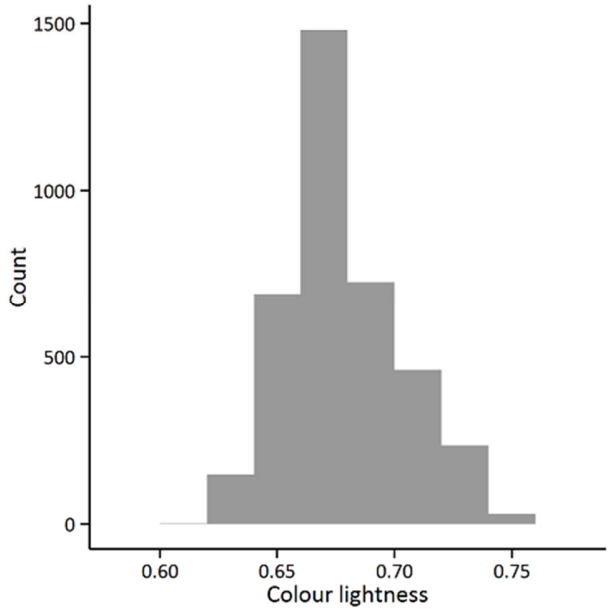

FIGURE 9.1.12. Histogram of the color lightness of geometrid moth assemblages.

References

Abrego, N., C. Bässler, M. Christensen, and J. Heilmann-Clausen. 2015. Implications of reserve size and forest connectivity for the conservation of wood-inhabiting fungi in Europe. Biological Conservation 191:469–477.

Abrego, N., M. Christensen, C. Bässler, A. M. Ainsworth, and J. Heilmann-Clausen. 2017. Understanding the distribution of wood-inhabiting fungi in European beech reserves from species-specific habitat models. Fungal Ecology 27, Part B:168–174.

Abrego, N., P. Oivanen, I. Viner, J. Nordén, R. Penttilä, A. Dahlberg, J. Heilmann-Clausen, P. Somervuo, O. Ovaskainen, and D. Schigel. 2016. Reintroduction of threatened fungal species via inoculation. Biological Conservation 203:120–124.

Abrego, N., and I. Salcedo. 2013. Variety of woody debris as the factor influencing wood-inhabiting fungal richness and assemblages: Is it a question of quantity or quality? Forest Ecology and Management 291:377–385.

Alexander, J. M., L. Chalmandrier, J. Lenoir, T. I. Burgess, F. Essl, S. Haider, C. Kueffer, K. McDougall, A. Milbau, M. A. Nuñez, A. Pauchard, W. Rabitsch, L. J. Rew, N. J. Sanders, and L. Pellissier. 2018. Lags in the response of mountain plant communities to climate change. Global Change Biology 24:563–579.

Ali, A., M. A. Rashid, Q. Y. Huang, and C.-L. Lei. 2016. Effect of UV-A radiation as an environmental stress on the development, longevity, and reproduction of the oriental armyworm, Mythimna separata (Lepidoptera: Noctuidae). Environmental Science and Pollution Research 23:17002–17007.

Ammer, C., A. Fichtner, A. Fischer, M. M. Gossner, P. Meyer, R. Seidl, F. M. Thomas, P. Annighöfer, J. Kreyling, B. Ohse, U. Berger, E. Feldmann, K.-H. Häberle, K. Heer, S. Heinrichs, F. Huth, K. Krämer-Klement, A. Mölder, J. Müller, M. Mund, L. Opgenoorth, P. Schall, M. Scherer-Lorenzen, D. Seidel, J. Vogt, and S. Wagner. 2018. Key ecological research questions for Central European forests. Basic and Applied Ecology.

Angert, A. L., L. G. Crozier, L. J. Rissler, S. E. Gilman, J. J. Tewksbury, and A. J. Chunco. 2011. Do species' traits predict recent shifts at expanding range edges? Ecology Letters 14:677–689.

Angilletta, M. J., B. S. Cooper, M. S. Schuler, and J. G. Boyles. 2010. The evolution of thermal physiology in endotherms. Frontiers in Bioscience (Elite Edition) 2:861–881.

Araujo, L. S., A. Komonen, and C. Lopes-Andrade. 2015. Influences of landscape structure on diversity of beetles associated with bracket fungi in Brazilian Atlantic Forest. Biological Conservation 191:659–666.

Arnold, P. A., P. Cassey, and C. R. White. 2017. Functional traits in red flour beetles: the dispersal phenotype is associated with leg length but not body size nor metabolic rate. Functional Ecology 31:653–661.

Arrese, E. L., and J. L. Soulages. 2010. Insect fat body: energy, metabolism, and regulation. Annual Review of Entomology 55:207–225.

Atkinson, D. 1994. Temperature and Organism Size—A Biological Law for Ectotherms? Pages 1–58 *in* M. Begon and A. H. Fitter, editors. Advances in Ecological Research. Academic Press.

Atkinson, D., and R. M. Sibly. 1997. Why are organisms usually bigger in colder environments?

Making sense of a life history puzzle. Trends in Ecology & Evolution 12:235–239.

Aukema, B., and C. Rieger. 1995. Catalogue of the Heteroptera of the Palaearctic Region - Vol. 1: Enicocephalomorpha, Dipsocoromorpha, Nepomorpha, Gerromorpha and Leptopodomorpha. Netherlands Entomological Society, Amsterdam.

Aukema, B., and C. Rieger. 1996. Catalogue of the Heteroptera of the Palaearctic Region - Vol. 2: Cimicomorpha 1. Netherlands Entomological Society, Amsterdam.

Aukema, B., and C. Rieger. 1999. Catalogue of the Heteroptera of the Palaearctic Region - Vol. 3: Cimicomorpha 2. Netherlands Entomological Society, Amsterdam.

Aukema, B., and C. Rieger. 2001. Catalogue of the Heteroptera of the Palaearctic Region - Vol. 4: Pentatomomorpha I. Netherlands Entomological Society, Amsterdam.

Aukema, B., and C. Rieger. 2006. Catalogue of the Heteroptera of the Palaearctic Region - Vol. 5: Pentatomomorpha II. Netherlands Entomological Society, Amsterdam.

Avila-Cabadilla, L. D., K. E. Stoner, M. Henry, and M. Y. A. Añorve. 2009. Composition, structure and diversity of phyllostomid bat assemblages in different successional stages of a tropical dry forest. Forest Ecology and Management 258:986–996.

Barbati, A., M. Marchetti, G. Chirici, and P. Corona. 2014. European Forest Types and Forest Europe SFM indicators: Tools for monitoring progress on forest biodiversity conservation. Forest Ecology and Management 321:145–157.

Barger, M. A., and G. W. Esch. 2002. Host specificity and the distribution-abundance relationship in a community of parasites infecting fishes in streams of North Carolina. The Journal of Parasitology 88:446–453.

Barton, K. 2015. MuMIn: Multi-model inference. R package version 1.15.5. http://CRAN.R-project.org/package=MuMIn.

Baselga, A. 2010. Partitioning the turnover and nestedness components of beta diversity. Global Ecology and Biogeography 19:134–143.

Baselga, A. 2013. Separating the two components of abundance-based dissimilarity: balanced changes in abundance vs. abundance gradients. Methods in Ecology and Evolution 4:552–557.

Baselga, A., D. Orme, S. Villeger, J. De Bortoli, and F. Leprieur. 2017. betapart: Partitioning Beta Diversity into Turnover and Nestedness Components. R package version 1.4-1.

Bässler, C. 2004. Das Klima im Nationalpark Bayerischer Wald - Darstellung, Entwicklung und Auswirkung. Nationalparkverwaltung Bayerischer Wald.

Bässler, C., R. Ernst, M. Cadotte, C. Heibl, and J. Müller. 2014. Near-to-nature logging influences fungal community assembly processes in a temperate forest. Journal of Applied Ecology 51:939–948.

Bässler, C., B. Förster, C. Moning, and J. Müller. 2009. The BIOKLIM-Project: biodiversity research between climate change and wilding in a temperate montane forest–the conceptual framework. Waldökologie, Landschaftsforschung und Naturschutz 7:21–33.

Bässler, C., T. Hothorn, R. Brandl, and J. Müller. 2013. Insects Overshoot the Expected Upslope Shift Caused by Climate Warming. PLoS ONE 8:e65842.

Bässler, C., J. Müller, F. Dziock, and R. Brandl. 2010a. Effects of resource availability and climate on the diversity of wood-decaying fungi. Journal of Ecology 98:822–832.

Bässler, C., J. Müller, T. Hothorn, T. Kneib, F. Badeck, and F. Dziock. 2010b. Estimation of the extinction risk for high-montane species as a consequence of global warming and assessment of their suitability as cross-taxon indicators. Ecological Indicators 10:341–352.

Bässler, C., L. Seifert, and J. Müller. 2015. The BIOKLIM Project in the National Park Bavarian Forest: Lessons from a biodiversity survey. Silva Gabreta 21:12.

Bates, D., M. Maechler, and B. Bolker. 2013. lme4: Linear mixed-effects models using S4 classes. R package version 0.999999-2. http://CRAN.R-project.org/package=lme4.

Begon, M., M. Mortimer, and D. J. Thompson. 1996. Population Ecology: A Unified Study of Animals and Plants. 3 edition. Wiley-Blackwell, Oxford ; Malden, MA.

Betts, C. R., and R. J. Wootton. 1988. Wing Shape and Flight Behaviour in Butterflies (Lepidoptera: Papilionoidea and Hesperioidea): A Preliminary Analysis. Journal of Experimental Biology 138:271–288.

Betts, M. G., B. Phalan, S. J. K. Frey, J. S. Rousseau, and Z. Yang. 2017. Old-growth forests buffer climate-sensitive bird populations from warming. Diversity and Distributions 24:439–447.

Bishop, T. R., M. P. Robertson, H. Gibb, B. J. van Rensburg, B. Braschler, S. L. Chown, S. H. Foord, T. C. Munyai, I. Okey, P. G. Tshivhandekano, V. Werenkraut, and C. L. Parr. 2016. Ant assemblages have darker and larger members in cold environments. Global Ecology and Biogeography 25:1489–1499.

Bivand, R., M. Altman, L. Anselin, R. Assunção, O. Berke, A. Bernat, G. Blanchet, E. Blankmeyer, M. Carvalho, B. Christensen, Y. Chun, C. Dormann, S. Dray, V. Gómez-Rubio, M. Gubri, R. Halbersma, E. Krainski, P. Legendre, N. Lewin-Koh, H. Li, J. Ma, A. Mallik, G. Millo, W. Mueller, H. Ono, P. Peres-Neto, G. Piras, M. Reder, M. Tiefelsdorf, R. Westerholt, and D. Yu. 2018. spdep: Spatial Dependence: Weighting Schemes, Statistics and Models.

Bivand, R., and C. Rundel. 2016. rgeos: Interface to Geometry Engine - Open Source (GEOS).

Blackburn, T. M., V. K. Brown, B. M. Doube, J. J. D. Greenwood, J. H. Lawton, and N. E. Stork. 1993. The Relationship between Abundance and Body Size in Natural Animal Assemblages. Journal of Animal Ecology 62:519–528.

Blackburn, T. M., P. Cassey, and K. J. Gaston. 2006. Variations on a theme: sources of heterogeneity in the form of the interspecific relationship between abundance and distribution. Journal of Animal Ecology 75:1426–1439.

Blackburn, T. M., and R. P. Duncan. 2001. Determinants of establishment success in introduced birds. Nature 414:195–197.

Blanchard, J. L., C. Mills, S. Jennings, C. J. Fox, B. D. Rackham, P. D. Eastwood, and C. M. O'Brien. 2005. Distribution–abundance relationships for North Sea Atlantic cod (Gadus morhua): observation versus theory. Canadian Journal of Fisheries and Aquatic Sciences 62:2001–2009.

Blüthgen, N., C. F. Dormann, D. Prati, V. H. Klaus, T. Kleinebecker, N. Hölzel, F. Alt, S. Boch, S. Gockel, A. Hemp, J. Müller, J.

Nieschulze, S. C. Renner, I. Schöning, U. Schumacher, S. A. Socher, K. Wells, K. Birkhofer, F. Buscot, Y. Oelmann, C. Rothenwöhrer, C. Scherber, T. Tscharntke, C. N. Weiner, M. Fischer, E. K. V. Kalko, K. E. Linsenmair, E.-D. Schulze, and W. W. Weisser. 2012. A quantitative index of land-use intensity in grasslands: Integrating mowing, grazing and fertilization. Basic and Applied Ecology 13:207–220.

Bodin, J., V. Badeau, E. Bruno, C. Cluzeau, J.-M. Moisselin, G.-R. Walther, and J.-L. Dupouey. 2013. Shifts of forest species along an elevational gradient in Southeast France: climate change or stand maturation? Journal of Vegetation Science 24:269–283.

Bogert, C. M. 1949. Thermoregulation in Reptiles, A Factor in Evolution. Evolution 3:195–211.

Boggs, C. L. 2009. Understanding insect life histories and senescence through a resource allocation lens. Functional Ecology 23:27–37.

Boggs, C. L., and K. D. Freeman. 2005. Larval food limitation in butterflies: effects on adult resource allocation and fitness. Oecologia 144:353–361.

Bojková, J., H. Čížková, A. Kučerová, V. Rádková, T. Soldán, R. Svidenský, and J. Vrba. 2015. Monitoring of the restored streams in the Vltavský Luh (Šumava national Park). Silva Gabreta 21:73–79.

Bojková, J., L. Seifert, J. Petruželová, V. Šorfová, V. Syrovátka, P. Sroka, and V. Polášková. 2018. Species richness and composition of macroinvertebrate assemblages in the Bavarian Forest: Preliminary results of the stream monitoring. Silva Gabreta 24:171–211.

Bolker, B. M., M. E. Brooks, C. J. Clark, S. W. Geange, J. R. Poulsen, M. H. H. Stevens, and J.-S. S. White. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends in Ecology & Evolution 24:127–135.

Borregaard, M. K., and C. Rahbek. 2010. Causality of the Relationship between Geographic Distribution and Species Abundance. The Quarterly Review of Biology 85:3–25.

Bouget, C., and P. Duelli. 2004. The effects of windthrow on forest insect communities: a literature review. Biological Conservation 118:281–299.

Bouget, C., G. Parmain, O. Gilg, T. Noblecourt, B. Nusillard, Y. Paillet, C. Pernot, L. Larrieu, and F. Gosselin. 2014. Does a set-aside conservation strategy help the restoration of old-growth forest attributes and recolonization by saproxylic beetles? Animal Conservation 17:342–353.

Braak, C. J. F. ter, A. Cormont, and S. Dray. 2012. Improved testing of species traits–environment relationships in the fourth-corner problem. Ecology 93:1525–1526.

Brändle, M., and R. Brandl. 2001a. Species richness of insects and mites on trees: expanding Southwood. Journal of Animal Ecology 70:491–504.

Brändle, M., and R. Brandl. 2001b. Distribution, abundance and niche breadth of birds: scale matters. Global Ecology and Biogeography 10:173–177.

Bräu, M., R. Bolz, H. Kolbeck, A. Nunner, J. Voith, and W. Wolf. 2013. Tagfalter in Bayern. Verlag Eugen Ulmer, Stuttgart (Hohenheim).

Brehm, G., and K. Fiedler. 2004. Bergmann's rule does not apply to geometrid moths along an elevational gradient in an Andean montane

rain forest. Global Ecology and Biogeography 13:7–14.

Brehm, G., D. Zeuss, and R. K. Colwell. 2018. Moth body size increases with elevation along a complete tropical elevational gradient for two hyperdiverse clades. Ecography 0.

Brooks, M. E., K. Kristensen, K. J. van Benthem, A. Magnusson, C. W. Berg, A. Nielsen, H. J. Skaug, M. Mächler, and B. M. Bolker. 2017. glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. The R Journal 9:378–400.

Brown, J. H. 1984. On the Relationship between Abundance and Distribution of Species. The American Naturalist 124:255–279.

Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West. 2004. Toward a Metabolic Theory of Ecology. Ecology 85:1771–1789.

Brunet, J., F. Örjan, and R. Gustav. 2010. Biodiversity in European beech forests–a review with recommendations for sustainable forest management. Ecological Bulletins:77–94.

Brus, D. J., G. M. Hengeveld, D. J. J. Walvoort, P. W. Goedhart, A. H. Heidema, G. J. Nabuurs, and K. Gunia. 2011. Statistical mapping of tree species over Europe. European Journal of Forest Research 131:145–157.

Buckley, L. B. 2008. Linking traits to energetics and population dynamics to predict lizard ranges in changing environments. The American Naturalist 171:E1–E19.

Buckley, L. B., M. C. Urban, M. J. Angilletta, L. G. Crozier, L. J. Rissler, and M. W. Sears. 2010. Can mechanism inform species' distribution models? Ecology Letters 13:1041–1054.

Burtt, E. H., and J. M. Ichida. 2004. GLOGER'S RULE, FEATHER-DEGRADING BACTERIA, AND COLOR VARIATION AMONG SONG SPARROWS. The Condor 106:681–687.

Butin, H. 1989. Krankheiten der Wald- und Parkbäume.

Cadotte, M. W. 2006. Dispersal and Species Diversity: A Meta-Analysis. The American Naturalist 167:913–924.

Cadotte, M. W., and C. M. Tucker. 2017. Should Environmental Filtering be Abandoned? Trends in Ecology & Evolution 32:429–437.

Campbell, J. L., and D. C. Donato. 2014. Trait-based approaches to linking vegetation and food webs in early-seral forests of the Pacific Northwest. Forest Ecology and Management 324:172–178.

Carlson, A. 2000. The effect of habitat loss on a deciduous forest specialist species: the White-backed Woodpecker (Dendrocopos leucotos). Forest Ecology and Management 131:215–221.

Caro, T. 2005. The Adaptive Significance of Coloration in Mammals. BioScience 55:125–136.

Casey, T. M., and B. A. Joos. 1983. Morphometrics, Conductance, Thoracic Temperature, and Flight Energetics of Noctuid and Geometrid Moths. Physiological Zoology 56:160–173.

Chao, A. 1987. Estimating the Population Size for Capture-Recapture Data with Unequal Catchability. Biometrics 43:783–791.

Chao, A., N. J. Gotelli, T. C. Hsieh, E. L. Sander, K. H. Ma, R. K. Colwell, and A. M. Ellison. 2014. Rarefaction and extrapolation with Hill numbers: a framework for sampling and

estimation in species diversity studies. Ecological Monographs 84:45–67.

CIPRA. 2007. Appell für eine zukunftsfähige Entwicklung der Bergwälder. Commission Internationale pour la Protection des Alpes. http://www.cipra.org.

Clobert, J., M. Baguette, T. G. Benton, and J. M. Bullock. 2012. Dispersal Ecology and Evolution. First Edition. Oxford University Press.

Clusella Trullas, S., J. H. van Wyk, and J. R. Spotila. 2007. Thermal melanism in ectotherms. Journal of Thermal Biology 32:235–245.

Corben, H. C. 1983. Wing-beat frequencies, wing-areas and masses of flying insects and hummingbirds. Journal of Theoretical Biology 102:611–623.

Cornwell, W. K., and D. D. Ackerly. 2009. Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. Ecological Monographs 79:109–126.

Council of the European Union. 1992. Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora. Page 206.

Cramer, M. J., and M. R. Willig. 2005. Habitat heterogeneity, species diversity and null models. Oikos 108:209–218.

Crozier, L., and G. Dwyer. 2006. Combining population-dynamic and ecophysiological models to predict climate-induced insect range shifts. The American Naturalist 167:853–866.

Curtis, R. J., T. M. Brereton, R. L. H. Dennis, C. Carbone, and N. J. B. Isaac. 2015. Butterfly abundance is determined by food availability and is mediated by species traits. Journal of Applied Ecology 52:1676–1684.

Dajoz, R., Université de Paris (1896-1968), and Faculté des sciences. 1966. Ecologie et biologie des coléoptères xylophages de la hêtraie. Vie et Milieu:637–763.

Dale, V. H., L. A. Joyce, S. McNulty, R. P. Neilson, M. P. Ayres, M. D. Flannigan, P. J. Hanson, L. C. Irland, A. E. Lugo, C. J. Peterson, D. Simberloff, F. J. Swanson, B. J. Stocks, and B. M. Wotton. 2001. Climate Change and Forest DisturbancesClimate change can affect forests by altering the frequency, intensity, duration, and timing of fire, drought, introduced species, insect and pathogen outbreaks, hurricanes, windstorms, ice storms, or landslides. BioScience 51:723–734.

Damuth, J. 1981. Population density and body size in mammals. Nature 290:699.

Darwin, C. 1859. On the origin of species.

Davis, A. K., B. D. Farrey, and S. Altizer. 2005. Variation in thermally induced melanism in monarch butterflies (Lepidoptera: Nymphalidae) from three North American populations. Journal of Thermal Biology 30:410–421.

Dieler, J., E. Uhl, P. Biber, J. Müller, T. Rötzer, and H. Pretzsch. 2017. Effect of forest stand management on species composition, structural diversity, and productivity in the temperate zone of Europe. European Journal of Forest Research 136:739–766.

Dirkx, G. H. P. 1998. Wood-pasture in Dutch Common woodlands and the deforestation of the Dutch landscape. Page *in* K. J. Kirby and C. Watkins, editors. The Ecological History of European Forests. CAB International, Nottingham.

Dobrovolski, R., A. S. Melo, F. A. S. Cassemiro, and J. A. F. Diniz-Filho. 2012. Climatic history and dispersal ability explain the relative importance of turnover and nestedness components of beta diversity. Global Ecology and Biogeography 21:191–197.

Doerfler, I., J. Müller, M. M. Gossner, B. Hofner, and W. W. Weisser. 2017. Success of a deadwood enrichment strategy in production forests depends on stand type and management intensity. Forest Ecology and Management 400:607–620.

Donato, D. C., J. L. Campbell, and J. F. Franklin. 2012. Multiple successional pathways and precocity in forest development: can some forests be born complex? Journal of Vegetation Science 23:576–584.

Dörnte, B., and D. Kües. 2013. Fast Microwave-based DNA Extraction from Vegetative Mycelium and Fruiting Body Tissues of Agaricomycetes for PCR Amplification. Current Trends in Biotechnology and Pharmacy 7:825–836.

Dray, S., and A.-B. Dufour. 2007. The ade4 Package: Implementing the Duality Diagram for Ecologists. Journal of Statistical Software 22:1–20.

Dray, S., and P. Legendre. 2008. Testing the Species Traits–Environment Relationships: The Fourth-Corner Problem Revisited. Ecology 89:3400–3412.

Drössler, L., and P. Meyer. 2006. Waldentwicklungsphasen in zwei Buchen-Urwaldreservaten in der Slowakei. Forstarchiv:155–161.

Dubovskiy, I. M., M. M. A. Whitten, V. Y. Kryukov, O. N. Yaroslavtseva, E. V. Grizanova, C. Greig, K. Mukherjee, A. Vilcinskas, P. V. Mitkovets, V. V. Glupov, and T. M. Butt. 2013. More than a color change: insect melanism, disease resistance and fecundity. Proceedings of the Royal Society B: Biological Sciences 280:20130584.

Dufour, P. C., K. R. Willmott, P. S. Padrón, S. Xing, T. C. Bonebrake, and B. R. Scheffers. 2018. Divergent melanism strategies in Andean butterfly communities structure diversity patterns and climate responses. Journal of Biogeography 45:2471–2482.

Ebert, G., and E. Rennwald. 1993a. Tagfalter I. corrected first edition. Verlag Eugen Ulmer, Stuttgart.

Ebert, G., and E. Rennwald. 1993b. Tagfalter II. corrected first edition. Verlag Eugen Ulmer, Stuttgart.

Eckelt, A., J. Müller, U. Bense, H. Brustel, H. Bußler, Y. Chittaro, L. Cizek, A. Frei, E. Holzer, M. Kadej, M. Kahlen, F. Köhler, G. Möller, H. Mühle, A. Sanchez, U. Schaffrath, J. Schmidl, A. Smolis, A. Szallies, T. Németh, C. Wurst, S. Thorn, R. H. B. Christensen, and S. Seibold. 2018. "Primeval forest relict beetles" of Central Europe: a set of 168 umbrella species for the protection of primeval forest remnants. Journal of Insect Conservation 22:15–28.

Edgar, R. C. 2010. Search and clustering orders of magnitude faster than BLAST. Bioinformatics 26:2460–2461.

Ellers, J., and C. L. Boggs. 2004. Functional ecological implications of intraspecific differences in wing melanization in Colias butterflies. Biological Journal of the Linnean Society 82:79–87.

Enquist, B. J., J. H. Brown, and G. B. West. 1998. Allometric scaling of plant energetics and population density. Nature 395:163–165.

Enquist, B. J., J. Norberg, S. P. Bonser, C. Violle, C. T. Webb, A. Henderson, L. L. Sloat, and V. M. Savage. 2015. Scaling from Traits to Ecosystems: Developing a General Trait Driver Theory via Integrating Trait-Based and Metabolic Scaling Theories. Pages 249–318 *in* S. Pawar, G. Woodward, and A. I. Dell, editors. Advances in Ecological Research. Academic Press.

Estrada, A., I. Morales-Castilla, P. Caplat, and R. Early. 2016. Usefulness of Species Traits in Predicting Range Shifts. Trends in Ecology & Evolution 31:190–203.

Fahrig, L. 2013. Rethinking patch size and isolation effects: the habitat amount hypothesis. Journal of Biogeography 40:1649–1663.

Faulks, L., R. Svanback, H. Ragnarsson-Stabo, P. Eklov, and O. Ostman. 2015. Intraspecific Niche Variation Drives Abundance-Occupancy Relationships in Freshwater Fish Communities. American Naturalist 186:272–283.

Faustmann, M. 1995. Calculation of the value which forest land and immature stands possess for forestry. Journal of Forest Economics (Sweden).

Ferrier, S., G. Manion, J. Elith, and K. Richardson. 2007. Using generalized dissimilarity modelling to analyse and predict patterns of beta diversity in regional biodiversity assessment. Diversity and Distributions 13:252–264.

Filipiak, M., Ł. Sobczyk, and J. Weiner. 2016. Fungal Transformation of Tree Stumps into a Suitable Resource for Xylophagous Beetles via Changes in Elemental Ratios. Insects 7:13.

Fischer, M., O. Bossdorf, S. Gockel, F. Hänsel, A. Hemp, D. Hessenmöller, G. Korte, J. Nieschulze, S. Pfeiffer, D. Prati, S. Renner, I. Schöning, U. Schumacher, K. Wells, F. Buscot, E. K. V. Kalko, K. E. Linsenmair, E.-D. Schulze, and W. W. Weisser. 2010. Implementing large-scale and long-term functional biodiversity research: The Biodiversity Exploratories. Basic and Applied Ecology 11:473–485.

Fox, J., and S. Weisberg. 2011. An R Companion to Applied Regression, Second Edition. Sage, Thousand Oaks, CA.

Franklin, J. F., T. A. Spies, R. V. Pelt, A. B. Carey, D. A. Thornburgh, D. R. Berg, D. B. Lindenmayer, M. E. Harmon, W. S. Keeton, D. C. Shaw, K. Bible, and J. Chen. 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. Forest Ecology and Management 155:399–423.

Fretwell, S. D., and H. L. Lucas. 1969. On territorial behavior and other factors influencing habitat distribution in birds. Acta Biotheoretica 19:16–36.

Friess, N., M. M. Gossner, W. W. Weisser, R. Brandl, and M. Brändle. 2017. Habitat availability drives the distribution–abundance relationship in phytophagous true bugs in managed grasslands. Ecology 98:2561–2573.

Full, R. J. 1997. Invertebrate locomotor systems. Page *in* W. H. Dantzler, editor. Handbook of Physiology. Oxford University Press, New York.

Gaston, K. J., T. M. Blackburn, J. J. D. Greenwood, R. D. Gregory, R. M. Quinn, and J. H. Lawton. 2000. Abundance–occupancy relationships. Journal of Applied Ecology 37:39–59.

Gaston, K. J., T. M. Blackburn, and R. D. Gregory. 1997a. Abundance-range size relationships of breeding and wintering birds in Britain: a comparative analysis. Ecography 20:569–579.

Gaston, K. J., T. M. Blackburn, and J. H. Lawton. 1997b. Interspecific Abundance-Range Size Relationships: An Appraisal of Mechanisms. The Journal of Animal Ecology 66:579.

Gaston, K. J., and J. H. Lawton. 1988. Patterns in Body Size, Population Dynamics, and Regional Distribution of Bracken Herbivores. The American Naturalist 132:662–680.

Gaston, K. J., and J. H. Lawton. 1990. Effects of Scale and Habitat on the Relationship between Regional Distribution and Local Abundance. Oikos 58:329–335.

Gates, D. M. 2003. Biophysical Ecology. Reprint edition. Dover Publications, Mineola, N.Y.

Gillooly, J. F., J. H. Brown, G. B. West, V. M. Savage, and E. L. Charnov. 2001. Effects of Size and Temperature on Metabolic Rate. Science 293:2248–2251.

Gillooly, J. F., E. L. Charnov, G. B. West, V. M. Savage, and J. H. Brown. 2002. Effects of size and temperature on developmental time. Nature 417:70–73.

Giraudoux, P., J.-P. Antonietti, C. Beale, D. Pleydell, and M. Treglia. 2018. pgirmess: Spatial Analysis and Data Mining for Field Ecologists.

Gloger, C. L. 1833. Das Abändern der Vögel durch Einfluss es Klimas. Akademische Buchdruckerei zu Berlin, Breslau.

Gonzalez, A. 2005. Local and regional community dynamics in fragmented landscapes. Pages 146–169 *in* M. Holyoak, M. Leibold, and R. Holt, editors. Metacommunities: spatial dynamics and ecological communities. University of Chicago Press, Chicago.

Gonzalez, A., J. H. Lawton, F. S. Gilbert, T. M. Blackburn, and I. Evans-Freke. 1998. Metapopulation Dynamics, Abundance, and Distribution in a Microecosystem. Science 281:2045–2047.

Gossner, M. M., N. K. Simons, R. Achtziger, T. Blick, W. H. . Dorow, F. Dziock, F. Köhler, W. Rabitsch, and W. W. Weisser. 2015a. A summary of eight traits of Coleoptera, Hemiptera, Orthoptera and Araneae, occurring in grasslands in Germany. Scientific Data 2.

Gossner, M. M., N. K. Simons, L. Höck, and W. W. Weisser. 2015b. Morphometric measures of Heteroptera sampled in grasslands across three regions of Germany. Ecology 96:1154–1154.

Gotelli, N. J., and R. K. Colwell. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters 4:379–391.

Goulson, D. 1994. Determination of larval melanization in the moth, *Mamestra brassicae*, and the role of melanin in thermoregulation. Heredity 73:471–479.

Graves, R. C. 1960. Ecological Observations on the Insects and Other Inhabitants of Woody Shelf Fungi (Basidiomycetes: Polyporaceae) in the Chicago Area. Annals of the Entomological Society of America 53:61–78.

Greenland, D., 1940-, D. G. (Douglas G. Goodin, R. C. (Raymond C. Smith, and 1934-. 2003. Climate variability and ecosystem response at long-term ecological research sites. Oxford University Press.

Gregory, R. D., and K. J. Gaston. 2000. Explanations of commonness and rarity in British breeding birds: separating resource use and resource availability. Oikos 88:515–526.

Grime, J. P. 2006. Trait convergence and trait divergence in herbaceous plant communities:

Mechanisms and consequences. Journal of Vegetation Science 17:255–260.

Grueber, C. E., S. Nakagawa, R. J. Laws, and I. G. Jamieson. 2011. Multimodel inference in ecology and evolution: challenges and solutions. Journal of Evolutionary Biology 24:699–711.

Gyllenberg, M., and I. Hanski. 1992. Single-species metapopulation dynamics: A structured model. Theoretical Population Biology 42:35–61.

Hannah, L. 2008. Protected Areas and Climate Change. Annals of the New York Academy of Sciences 1134:201–212.

Hansen, M. C., P. V. Potapov, R. Moore, M. Hancher, S. A. Turubanova, A. Tyukavina, D. Thau, S. V. Stehman, S. J. Goetz, T. R. Loveland, A. Kommareddy, A. Egorov, L. Chini, C. O. Justice, and J. R. G. Townshend. 2013. High-Resolution Global Maps of 21st-Century Forest Cover Change. Science 342:850–853.

Hanski, I. 1991. Single-species metapopulation dynamics: concepts, models and observations. Biological Journal of the Linnean Society 42:17–38.

Hanski, I. 1999. Metapopulation Ecology. Oxford University Press.

Hanski, I., and M. Gyllenberg. 1993. Two General Metapopulation Models and the Core-Satellite Species Hypothesis. The American Naturalist 142:17–41.

Hanski, I., J. Kouki, and A. Halkka. 1993. Three explanations of the positive relationship between distribution and abundance of species. Species diversity in ecological communities: historical and geographical perspectives:108–116.

Harrison, X. A. 2014. Using observation-level random effects to model overdispersion in count data in ecology and evolution. PeerJ 2:e616.

Hartl, D. L., and A. G. Clark. 2006. Principles of Population Genetics. 4th edition. Sinauer Associates is an imprint of Oxford University Press, Sunderland, Mass.

Harvey, P., and M. Pagel. 1991. The comparative method in evolutionary biology. 1 edition. Oxford University Press.

Hawkins, B. A., B. Leroy, M. Á. Rodríguez, A. Singer, B. Vilela, F. Villalobos, X. Wang, and D. Zelený. 2017. Structural bias in aggregated species-level variables driven by repeated species co-occurrences: a pervasive problem in community and assemblage data. Journal of Biogeography 44:1199–1211.

Heidrich, L., N. Friess, K. Fiedler, M. Brändle, A. Hausmann, R. Brandl, and D. Zeuss. 2018. The dark side of Lepidoptera: Color lightness of geometrid moths decreases with increasing latitude. Global Ecology and Biogeography 27:407–416.

Heikkala, O., P. Martikainen, and J. Kouki. 2016. Decadal effects of emulating natural disturbances in forest management on saproxylic beetle assemblages. Biological Conservation 194:39–47.

Heilmann-Clausen, J., E. Aude, K. van Dort, M. Christensen, A. Piltaver, M. Veerkamp, R. Walleyn, I. Siller, T. Standovar, and P. Odor. 2014. Communities of wood-inhabiting bryophytes and fungi on dead beech logs in Europe - reflecting substrate quality or shaped by climate and forest conditions? Journal of Biogeography 41:2269–2282.

Heilmann-Clausen, J., E. S. Barron, L. Boddy, A. Dahlberg, G. W. Griffith, J. Nordén, O. Ovaskainen, C. Perini, B. Senn-Irlet, and P. Halme. 2015. A fungal perspective on conservation biology. Conservation Biology 29:61–68.

Heino, J. 2005. Positive relationship between regional distribution and local abundance in stream insects: a consequence of niche breadth or niche position? Ecography 28:345–354.

Heino, J., and J. Soininen. 2006. Regional occupancy in unicellular eukaryotes: a reflection of niche breadth, habitat availability or size-related dispersal capacity? Freshwater Biology 51:672–685.

Heinrich, B. 1993. The Hot-Blooded Insects: Strategies and Mechanisms of Thermoregulation. Springer-Verlag, Berlin Heidelberg.

Heurich, M., B. Beudert, H. Rall, and Z. Křenová. 2010. National Parks as Model Regions for Interdisciplinary Long-Term Ecological Research: The Bavarian Forest and Šumavá National Parks Underway to Transboundary Ecosystem Research. Pages 327–344 Long-Term Ecological Research. Springer, Dordrecht.

Heurich, M., and M. Neufanger. 2005. Die Wälder des Nationalparks Bayerischer Wald. Ergebnisse der Waldinventur 2002/2003 im geschichtlichen und waldökologischen Kontext. Nationalparkverwaltung Bayerischer Wald, Grafenau.

Heurich, M., and F. Thoma. 2008. Estimation of forestry stand parameters using laser scanning data in temperate, structurally rich natural European beech (Fagus sylvatica) and Norway spruce (Picea abies) forests. Forestry: An International Journal of Forest Research 81:645–661.

Hijmans, R. J. 2016. geosphere: Spherical Trigonometry. R package version 1.5-5.

Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis. 2005. Very high resolution interpolated climate surfaces for global land areas. International journal of climatology 25:1965–1978.

Hijmans, R. J., J. van Etten, J. Cheng, M. Mattiuzzi, M. Sumner, J. A. Greenberg, O. P. Lamigueiro, A. Bevan, E. B. Racine, and A. Shortridge. 2016. raster: Geographic Data Analysis and Modeling.

Hill, C. J. 1989. The effect of adult diet on the biology of butterflies : 2. The common crow butterfly, Euploea core corinna. Oecologia 81:258–266.

Hill, M. O. 1973. Diversity and Evenness: A Unifying Notation and Its Consequences. Ecology 54:427–432.

Hilmers, T., C. Bässler, N. Friess, M. Heurich, J. Müller, and L. Seifert. 2018a. Changes in forest structure in the Bavarian Forest National Park – an evaluation after 10 years of the BIO-KLIM-Project. Silva Gabreta 24:161–170.

Hilmers, T., N. Friess, C. Bässler, M. Heurich, R. Brandl, H. Pretzsch, R. Seidl, and J. Müller. 2018b. Biodiversity along temperate forest succession. Journal of Applied Ecology.

Holm, S., R. B. Davis, J. Javoiš, E. Õunap, A. Kaasik, F. Molleman, and T. Tammaru. 2016. A comparative perspective on longevity: the effect of body size dominates over ecology in moths. Journal of Evolutionary Biology 29:2422–2435.

Holt, A. R., K. J. Gaston, and F. He. 2002. Occupancy-abundance relationships and spatial

distribution: A review. Basic and Applied Ecology 3:1–13.

Holyoak, M., M. A. Leibold, and R. D. Holt. 2005. Metacommunities: Spatial Dynamics And Ecological Communities. New edition. University of Chicago Press, Chicago.

Honěk, A. 1993. Intraspecific Variation in Body Size and Fecundity in Insects: A General Relationship. Oikos 66:483–492.

Horne, C. R., A. G. Hirst, and D. Atkinson. 2015. Temperature-size responses match latitudinal-size clines in arthropods, revealing critical differences between aquatic and terrestrial species. Ecology Letters 18:327–335.

Hothorn, T., F. Bretz, P. Westfall, R. M. Heiberger, A. Schuetzenmeister, and S. Scheibe. 2016. multcomp: Simultaneous Inference in General Parametric Models.

Hsieh, T. C., K. H. Ma, and A. Chao. 2016. iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). Methods in Ecology and Evolution 7:1451–1456.

Hubbell, S. P. 2001. The Unified Neutral Theory of Biodiversity and Biogeography. Princeton University Press.

Hurlbert, A. H. 2004. Species–energy relationships and habitat complexity in bird communities. Ecology Letters 7:714–720.

Hutchinson, G. 1957. Population Studies - Animal Ecology and Demography - Concluding Remarks. Cold Spring Harbor Symposia on Quantitative Biology 22:415–427.

Jacobs, J. M., J. R. Spence, and D. W. Langor. 2007. Influence of boreal forest succession and dead wood qualities on saproxylic beetles. Agricultural and Forest Entomology 9:3–16.

Jiménez-Alfaro, B., M. Girardello, M. Chytrý, J.-C. Svenning, W. Willner, J.-C. Gégout, E. Agrillo, J. A. Campos, U. Jandt, Z. Kącki, U. Šilc, M. Slezák, L. Tichý, I. Tsiripidis, P. D. Turtureanu, M. Ujházyová, and T. Wohlgemuth. 2018. History and environment shape species pools and community diversity in European beech forests. Nature Ecology & Evolution 2:483.

Jonsell, M., and G. Nordlander. 2004. Host selection patterns in insects breeding in bracket fungi. Ecological Entomology 29:697–705.

Jonsson, M. 2003. Colonisation ability of the threatened tenebrionid beetle Oplocephala haemorrhoidalis and its common relative Bolitophagus reticulatus. Ecological Entomology 28:159–167.

Jost, L. 2007. Partitioning Diversity into Independent Alpha and Beta Components. Ecology 88:2427–2439.

Judova, J., K. Dubikova, S. Gaperova, J. Gaper, and P. Pristas. 2012. The occurrence and rapid discrimination of Fomes fomentarius genotypes by ITS-RFLP analysis. Fungal Biology 116:155–160.

Jung, B. H., S. Y. Kim, and J. I. Kim. 2007. Taxonomic review of the tribe Bolitophagini in Korea (Coleoptera: Tenebrionidae: Tenebrioninae). Entomological Research 37:190–196.

Kalmus, H. 1941. Physiology and Ecology of Cuticle Color in Insects. Nature 148:428–431.

Kaplan, J. O., K. M. Krumhardt, and N. Zimmermann. 2009. The prehistoric and preindustrial deforestation of Europe. Quaternary Science Reviews 28:3016–3034.

Karl, I., S. A. Janowitz, and K. Fischer. 2008. Altitudinal life-history variation and thermal adaptation in the copper butterfly Lycaena tityrus. Oikos 117:778–788.

Kearney, M., and W. Porter. 2009. Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. Ecology Letters 12:334–350.

Kearney, M. R., A. P. Isaac, and W. P. Porter. 2014. microclim: Global estimates of hourly microclimate based on long-term monthly climate averages. Scientific Data 1:140006.

Keddy, P. A. 1992. A Pragmatic Approach to Functional Ecology. Functional Ecology 6:621–626.

Kim, W., T. Gilet, and J. W. M. Bush. 2011. Optimal concentrations in nectar feeding. Proceedings of the National Academy of Sciences 108:16618–16621.

Kissling, W. D., and G. Carl. 2008. Spatial autocorrelation and the selection of simultaneous autoregressive models. Global Ecology and Biogeography 17:59–71.

Kobayashi, T., and T. Sota. 2016. Distance decay of similarity in fungivorous insect communities: assessing dispersal limitation using genetic data. Ecosphere 7:e01358.

Komonen, A. 2001. Structure of insect communities inhabiting old-growth forest specialist bracket fungi. Ecological Entomology 26:63–75.

Komonen, A., and J. Müller. 2018. Dispersal ecology of deadwood organisms and connectivity conservation. Conservation Biology 32:535–545.

Kooijman, S. a. L. M., T. Sousa, L. Pecquerie, J. V. D. Meer, and T. Jager. 2008. From food-dependent statistics to metabolic parameters, a practical guide to the use of dynamic energy budget theory. Biological Reviews 83:533–552.

Kotze, D. J., J. Niemelä, R. B. O'Hara, and H. Turin. 2003. Testing abundance-range size relationships in European carabid beetles (Coleoptera, Carabidae). Ecography 26:553–566.

Kouki, J., E. Hyvärinen, H. Lappalainen, P. Martikainen, and M. Similä. 2012. Landscape context affects the success of habitat restoration: large-scale colonization patterns of saproxylic and fire-associated species in boreal forests. Diversity and Distributions 18:348–355.

Kraft, N. J. B., P. B. Adler, O. Godoy, E. C. James, S. Fuller, and J. M. Levine. 2015. Community assembly, coexistence and the environmental filtering metaphor. Functional Ecology 29:592–599.

Krah, F.-S., S. Seibold, R. Brandl, P. Baldrian, J. Müller, and C. Bässler. 2018. Independent effects of host and environment on the diversity of wood-inhabiting fungi. Journal of Ecology.

Krenn, H. W. 2010. Feeding Mechanisms of Adult Lepidoptera: Structure, Function, and Evolution of the Mouthparts. Annual review of entomology 55:307–327.

Křenová, Z., and L. Seifert. 2015. SILVA GABRETA – monitoring of mountain ecosystems. Silva Gabreta 21:1–4.

Křenová, Z., and L. Seifert. 2018. The Silva Gabreta Project - transboundary cooperation in moinitoring of biodiversity and water regime. Silva Gabreta 24:1–20.

Kudrna, O., A. Harpke, C. Kux, J. Pennerstorfer, O. Schweiger, and J. Settele. 2011.

Distribution Atlas of Butterflies in Europe. Gesellschaft für Schmetterlingsschutz, Halle, Germany.

Kuusinen, M., and J. Siitonen. 1998. Epiphytic lichen diversity in old-growth and managed Picea abies stands in southern Finland. Journal of Vegetation Science 9:283–292.

Larrieu, L., Y. Paillet, S. Winter, R. Bütler, D. Kraus, F. Krumm, T. Lachat, A. K. Michel, B. Regnery, and K. Vandekerkhove. 2018. Tree related microhabitats in temperate and Mediterranean European forests: A hierarchical typology for inventory standardization. Ecological Indicators 84:194–207.

Larsson, T. 2001. Biodiversity evaluation tools for European forests. A report from the FAIR project Indicators for monitoring and evaluation of forest biodiversity in Europe. Ecological Bulletins 50.

Laughlin, D. C., and J. Messier. 2015. Fitness of multidimensional phenotypes in dynamic adaptive landscapes. Trends in Ecology & Evolution 30:487–496.

Laughlin, D. C., R. T. Strahan, P. B. Adler, and M. M. Moore. 2018. Survival rates indicate that correlations between community-weighted mean traits and environments can be unreliable estimates of the adaptive value of traits. Ecology Letters 21:411–421.

Lawton, J. H. 1999. Are There General Laws in Ecology? Oikos 84:177–192.

Lefcheck, J. S. 2015. piecewiseSEM: Piecewise structural equation modelling in R for ecology, evolution, and systematics. Methods in Ecology and Evolution 7:573–579.

Legendre, P., and L. Legendre. 2012. Numerical Ecology. Second edition. Elsevier, Amsterdam.

Lehnert, L. W., C. Bässler, R. Brandl, P. J. Burton, and J. Müller. 2013. Conservation value of forests attacked by bark beetles: Highest number of indicator species is found in early successional stages. Journal for Nature Conservation 21:97–104.

Leighton, G. R. M., P. S. Hugo, A. Roulin, and A. Amar. 2016. Just Google it: assessing the use of Google Images to describe geographical variation in visible traits of organisms. Methods in Ecology and Evolution 7:1060–1070.

Lenoir, J., J.-C. Gégout, A. Guisan, P. Vittoz, T. Wohlgemuth, N. E. Zimmermann, S. Dullinger, H. Pauli, W. Willner, and J.-C. Svenning. 2010. Going against the flow: potential mechanisms for unexpected downslope range shifts in a warming climate. Ecography 33:295–303.

Lepetz, V., M. Massot, D. S. Schmeller, and J. Clobert. 2009. Biodiversity monitoring: some proposals to adequately study species' responses to climate change. Biodiversity and Conservation 18:3185.

Leray, M., and N. Knowlton. 2015. DNA barcoding and metabarcoding of standardized samples reveal patterns of marine benthic diversity. Proceedings of the National Academy of Sciences 112:2076–2081.

Levin, S. A. 1992. The Problem of Pattern and Scale in Ecology: The Robert H. MacArthur Award Lecture. Ecology 73:1943–1967.

Llandres, A. L., G. M. Marques, J. L. Maino, S. a. L. M. Kooijman, M. R. Kearney, and J. Casas. 2015. A dynamic energy budget for the whole life-cycle of holometabolous insects. Ecological Monographs 85:353–371.

Londo, G. 1976. The decimal scale for releves of permanent quadrats. Vegetatio 33:61–64.

MacArthur, R. H., and J. W. MacArthur. 1961. On Bird Species Diversity. Ecology 42:594–598.

MacArthur, R. H., and E. O. Wilson. 1967. The Theory of Island Biogeography. Princeton University Press.

Mackintosh, J. A. 2001. The Antimicrobial Properties of Melanocytes, Melanosomes and Melanin and the Evolution of Black Skin. Journal of Theoretical Biology 211:101–113.

MacLean, S. A., and S. R. Beissinger. 2017. Species' traits as predictors of range shifts under contemporary climate change: A review and meta-analysis. Global Change Biology 23:4094–4105.

Maestri, R., G. I. Shenbrot, and B. R. Krasnov. 2017. Parasite beta diversity, host beta diversity and environment: application of two approaches to reveal patterns of flea species turnover in Mongolia. Journal of Biogeography:n/a-n/a.

Magri, D. 2008. Patterns of post-glacial spread and the extent of glacial refugia of European beech (Fagus sylvatica). Journal of Biogeography 35:450–463.

Majerus, M. E. N. 1998. Melanism: Evolution in Action. 1 edition. Oxford University Press, Oxford ; New York.

Manion, G., M. Lisk, S. Ferrier, D. Nieto-Lugilde, K. Mokany, and M. C. Fitzpatrick. 2017. gdm: Generalized Dissimilarity Modeling. R package version 1.3.2.

Margules, C. R., and R. L. Pressey. 2000. Systematic conservation planning. Nature 405:243–253.

Maris, V., P. Huneman, A. Coreau, S. Kéfi, R. Pradel, and V. Devictor. 2018. Prediction in ecology: promises, obstacles and clarifications. Oikos 127:171–183.

Marshall, C. T., and K. T. Frank. 1995. Density-dependent habitat selection by juvenile haddock (Melanogrammus aeglefinus) on the southwestern Scotian Shelf. Canadian Journal of Fisheries and Aquatic Sciences 52:1007–1017.

Martin, K. J., and P. T. Rygiewicz. 2005. Fungal-specific PCR primers developed for analysis of the ITS region of environmental DNA extracts. BMC Microbiology 5:28.

Martin, M. 2011. Cutadapt removes adapter sequences from high-throughput sequencing reads. EMBnet.journal 17:10–12.

Matthewman, W. G., and D. P. Pielou. 1971. Arthropods inhabiting the sporophores of Fomes fomentarius (Polyporaceae) in Gatineau Park, Quebec. The Canadian Entomologist 103:775–847.

May, M. L. 1979. Insect Thermoregulation. Annual Review of Entomology 24:313–349.

McCreadie, J. W., and P. H. Adler. 2014. Abundance–occupancy relationships of larval black flies (Diptera: Simuliidae) in temperate Nearctic streams. Insect Conservation and Diversity 7:523–532.

McGill, B. J., B. J. Enquist, E. Weiher, and M. Westoby. 2006. Rebuilding community ecology from functional traits. Trends in Ecology & Evolution 21:178–185.

Mckinnon, J. S., and M. E. R. Pierotti. 2010. Color polymorphism and correlated characters: genetic mechanisms and evolution. Molecular Ecology 19:5101–5125.

McNeely, J. A., and K. R. Miller. 1983. IUCN, National Parks, and Protected Areas: Priorities for Action. Environmental Conservation 10:13–21.

Memmott, J., P. G. Craze, N. M. Waser, and M. V. Price. 2007. Global warming and the disruption of plant-pollinator interactions. Ecology Letters 10:710–717.

Merrill, W., and E. B. Cowling. 1966. Role of nitrogen in wood deterioration-amount and distribution of nitrogen in fungi. Phytopathology 56.

Mikkola, K., and M. J. Rantala. 2010. Immune defence, a possible nonvisual selective factor behind the industrial melanism of moths (Lepidoptera). Biological Journal of the Linnean Society 99:831–838.

Mikoláš, M., M. Tejkal, T. Kuemmerle, P. Griffiths, M. Svoboda, T. Hlásny, P. J. Leitão, and R. C. Morrissey. 2017. Forest management impacts on capercaillie (Tetrao urogallus) habitat distribution and connectivity in the Carpathians. Landscape Ecology 32:163–179.

Mills, L. S., M. E. Soulé, and D. F. Doak. 1993. The Keystone-Species Concept in Ecology and ConservationManagement and policy must explicitly consider the complexity of interactions in natural systems. BioScience 43:219–224.

Moning, C., and J. Müller. 2009. Critical forest age thresholds for the diversity of lichens, molluscs and birds in beech (Fagus sylvatica L.) dominated forests. Ecological Indicators 9:922–932.

Morin, P. J. 2011. Community Ecology. 2 edition. Wiley-Blackwell, Chichester, West Sussex ; Hoboken, NJ.

Morinière, J., B. C. de Araujo, A. W. Lam, A. Hausmann, M. Balke, S. Schmidt, L. Hendrich, D. Doczkal, B. Fartmann, S. Arvidsson, and G. Haszprunar. 2016. Species Identification in Malaise Trap Samples by DNA Barcoding Based on NGS Technologies and a Scoring Matrix. PLOS ONE 11:e0155497.

Morris, M. G. 1979. Responses of Grassland Invertebrates to Management by Cutting. II. Heteroptera. Journal of Applied Ecology 16:417–432.

Müller, J. 2005. Waldstrukturen als Steuergröße für Artengemeinschaften in kollinen bis submontanen Buchenwäldern. Universität München.

Müller, J., R. Brandl, M. Brändle, B. Förster, B. C. de Araujo, M. M. Gossner, A. Ladas, M. Wagner, M. Maraun, P. Schall, S. Schmidt, M. Heurich, S. Thorn, and S. Seibold. 2018. LiDAR-derived canopy structure supports the more-individuals hypothesis for arthropod diversity in temperate forests. Oikos 127:814–824.

Müller, J., J. Brunet, A. Brin, C. Bouget, H. Brustel, H. Bussler, B. Förster, G. Isacsson, F. Köhler, T. Lachat, and M. M. Gossner. 2013. Implications from large-scale spatial diversity patterns of saproxylic beetles for the conservation of European Beech forests. Insect Conservation and Diversity 6:162–169.

Müller, J., H. Bußler, M. Goßner, T. Rettelbach, and P. Duelli. 2008. The European spruce bark beetle Ips typographus in a national park: from pest to keystone species. Biodiversity and Conservation 17:2979.

Müller, J., R. F. Noss, H. Bussler, and R. Brandl. 2010. Learning from a "benign neglect strategy" in a national park: Response of saproxylic

beetles to dead wood accumulation. Biological Conservation 143:2559–2569.

Nagy, K. A., I. A. Girard, and T. K. Brown. 1999. Energetics of free-ranging mammals, reptiles, and birds. Annual Review of Nutrition 19:247–277.

Nakagawa, S., and H. Schielzeth. 2013. A general and simple method for obtaining R2 from generalized linear mixed-effects models. Methods in Ecology and Evolution 4:133–142.

Nee, S., R. D. Gregory, and R. M. May. 1991. Core and Satellite Species: Theory and Artefacts. Oikos 62:83–87.

Niven, J. E., and J. P. . Scharlemann. 2005. Do insect metabolic rates at rest and during flight scale with body mass? Biology Letters 1:346–349.

Nordén, J., J. Åström, T. Josefsson, S. Blumentrath, O. Ovaskainen, A. Sverdrup-Thygeson, and B. Nordén. 2018. At which spatial and temporal scales can fungi indicate habitat connectivity? Ecological Indicators 91:138–148.

Nowak, M. 2006. Evolutionary Dynamics: Exploring the Equations of Life. Harvard University Press, Cambridge, Mass.

O'Connor, R. J. 1987. Organization of avian assemblages: the influence of intraspecific habitat dynamics. Pages 163–183 *in* J. H. R. Gee and P. S. Giller, editors. Organization of Communities: Past and Present. Blackwell Scientific Publications, Oxford (UK).

Ódor, P., J. Heilmann-Clausen, M. Christensen, E. Aude, K. W. van Dort, A. Piltaver, I. Siller, M. T. Veerkamp, R. Walleyn, T. Standovár, A. F. M. van Hees, J. Kosec, N. Matočec, H. Kraigher, and T. Grebenc. 2006. Diversity of dead wood inhabiting fungi and bryophytes in semi-natural beech forests in Europe. Biological Conservation 131:58–71.

Ohgushi, T., O. Schmitz, and R. D. Holt. 2012. Trait-Mediated Indirect Interactions Ecological and Evolutionary Perspectives. Cambridge University Press, Cambridge.

Oksanen, J., F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, E. Szoecs, and H. Wagner. 2017. vegan: Community Ecology Package.

Oksanen, J., F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, E. Szoecs, and H. Wagner. 2018. vegan: Community Ecology Package. R package version 2.4-6. http://CRAN.R-project.org/package=vegan.

Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, and H. Wagner. 2015. vegan: Community Ecology Package. R package version 2.2-1. http://CRAN.R-project.org/package=vegan.

Oliver, C. D., and B. C. Larson. 1990. Forest stand dynamics. McGraw-Hill Pub., New York.

Östman, Ö. 2010. Abundance–occupancy relationships in metapopulations: examples of rock pool Daphnia. Oecologia 165:687–697.

Päivinen, J., A. Grapputo, V. Kaitala, A. Komonen, J. S. Kotiaho, K. Saarinen, and N. Wahlberg. 2005. Negative density-distribution relationship in butterflies. BMC Biology 3:5.

Palmer, M. A., E. S. Bernhardt, E. A. Chornesky, S. L. Collins, A. P. Dobson, C. S. Duke, B. D. Gold, R. B. Jacobson, S. E. Kingsland, R. H.

Kranz, M. J. Mappin, M. L. Martinez, F. Micheli, J. L. Morse, M. L. Pace, M. Pascual, S. S. Palumbi, O. J. Reichman, A. R. Townsend, and M. G. Turner. 2005. Ecological science and sustainability for the 21st century. Frontiers in Ecology and the Environment 3:4–11.

Parisi, A. V., M. G. Kimlin, J. C. F. Wong, and M. Wilson. 2000. Diffuse component of solar ultraviolet radiation in tree shade1Paper presented at the 2nd Online Conference for Photochemistry and Photobiology.1. Journal of Photochemistry and Photobiology B: Biology 54:116–120.

Parker, W. C., S. J. Colombo, M. L. Cherry, S. Greifenhagen, C. Papadopol, M. D. Flannigan, R. S. McAlpine, and T. Scarr. 2000. Third Millennium Forestry: What climate change might mean to forests and forest management in Ontario. The Forestry Chronicle 76:445–463.

Pearse, I. S., and F. Altermatt. 2013. Extinction cascades partially estimate herbivore losses in a complete Lepidoptera–plant food web. Ecology 94:1785–1794.

Pearse, W. D., A. M. Barbosa, S. A. Fritz, S. A. Keith, L. J. Harmon, J. Harte, D. Silvestro, X. Xiao, and T. J. Davies. 2018. Building up biogeography: Pattern to process. Journal of Biogeography 45:1223–1230.

Pechenik, J. A. 2006. Larval experience and latent effects—metamorphosis is not a new beginning. Integrative and Comparative Biology 46:323–333.

Pélisson, P.-F., M.-C. Bel-Venner, D. Giron, F. Menu, and S. Venner. 2013. From Income to Capital Breeding: When Diversified Strategies Sustain Species Coexistence. PLOS ONE 8:e76086.

Peña-Cuéllar, E. de la, K. E. Stoner, L. D. Avila-Cabadilla, M. Martínez-Ramos, and A. Estrada. 2012. Phyllostomid bat assemblages in different successional stages of tropical rain forest in Chiapas, Mexico. Biodiversity and Conservation 21:1381–1397.

Peura, M., R. Silveyra Gonzalez, J. Müller, M. Heurich, L. A. Vierling, M. Mönkkönen, and C. Bässler. 2016. Mapping a 'cryptic kingdom': Performance of lidar derived environmental variables in modelling the occurrence of forest fungi. Remote Sensing of Environment 186:428–438.

Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and R Core Team. 2017. nlme: Linear and Nonlinear Mixed Effects Models.

Pinkert, S., R. Brandl, and D. Zeuss. 2017. Color lightness of dragonfly assemblages across North America and Europe. Ecography 40:1110–1117.

Pinkert, S., K.-D. B. Dijkstra, D. Zeuss, C. Reudenbach, R. Brandl, and C. Hof. 2018. Evolutionary processes, dispersal limitation and climatic history shape current diversity patterns of European dragonflies. Ecography 41:795–804.

Pinkert, S., and D. Zeuss. 2018. Thermal Biology: Melanin-Based Energy Harvesting across the Tree of Life. Current biology: CB 28:R887–R889.

Potocký, P., A. Bartoňová, J. Beneš, M. Zapletal, and M. Konvička. 2018. Life-history traits of Central European moths: gradients of variation and their association with rarity and threats. Insect Conservation and Diversity 11:493–505.

Pristas, P., S. Gaperova, J. Gaper, and J. Judova. 2013. Genetic variability in Fomes fomentarius reconfirmed by translation elongation factor 1-

α DNA sequences and 25S LSU rRNA sequences. Biologia 68:816–820.

Prokkola, J., D. Roff, T. Kärkkäinen, I. Krams, and M. J. Rantala. 2013. Genetic and phenotypic relationships between immune defense, melanism and life-history traits at different temperatures and sexes in *Tenebrio molitor*. Heredity 111:89–96.

R Core Team. 2016. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

R Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Ralph, C. P. 1977. Effect of Host Plant Density on Populations of a Specialzied, Seed-Sucking Bug, Oncopeltus Fasciatus. Ecology 58:799–809.

Rannap, R., A. Lõhmus, and L. Briggs. 2009. Niche position, but not niche breadth, differs in two coexisting amphibians having contrasting trends in Europe. Diversity and Distributions 15:692–700.

Ratnasingham, S., and P. D. N. Hebert. 2007. bold: The Barcode of Life Data System (http://www.barcodinglife.org). Molecular Ecology Notes 7:355–364.

Redecker, D., T. M. Szaro, R. J. Bowman, and T. D. Bruns. 2001. Small genets of Lactarius xanthogalactus, Russula cremoricolor and Amanita francheti in late-stage ectomycorrhizal successions. Molecular Ecology 10:1025–1034.

Reibnitz, J. 1999. Verbreitung und Lebensräume der Baumschwammfresser Südwestdeutschlands (Coleoptera: Cisidae). Mitteilungen Entomologischer Verein Stuttgart:2–75.

Reich, P. B., M. B. Walters, and D. S. Ellsworth. 1997. From tropics to tundra: Global convergence in plant functioning. Proceedings of the National Academy of Sciences 94:13730–13734.

Reilly, J. R., A. E. Hajek, A. M. Liebhold, and R. Plymale. 2014. Impact of Entomophaga maimaiga (Entomophthorales: Entomophthoraceae) on Outbreak Gypsy Moth Populations (Lepidoptera: Erebidae): The Role of Weather. Environmental Entomology 43:632–641.

Revell, L. J. 2017. phytools: Phylogenetic Tools for Comparative Biology.

Riis, T., and K. Sand-Jensen. 2002. Abundance-range size relationships in stream vegetation in Denmark. Plant Ecology 161:175–183.

Robin, V., M.-J. Nadeau, P. M. Grootes, H.-R. Bork, and O. Nelle. 2016. Too early and too northerly: evidence of temperate trees in northern Central Europe during the Younger Dryas. New Phytologist 212:259–268.

Roff, D. A., and D. J. Fairbairn. 2013. The costs of being dark: the genetic basis of melanism and its association with fitness-related traits in the sand cricket. Journal of Evolutionary Biology 26:1406–1416.

Root, R. B. 1973. Organization of a Plant-Arthropod Association in Simple and Diverse Habitats: The Fauna of Collards (Brassica Oleracea). Ecological Monographs 43:95–124.

Root, R. B., and N. Cappuccino. 1992. Patterns in Population Change and the Organization of the Insect Community Associated with Goldenrod. Ecological Monographs 62:393–420.

Roulin, A. 2014. Melanin-based color polymorphism responding to climate change. Global Change Biology 20:3344–3350.

Rukke, B. A. 2000. Effects of habitat fragmentation: increased isolation and reduced habitat size reduces the incidence of dead wood fungi beetles in a fragmented forest landscape. Ecography 23:492–502.

Rumpf, S. B., K. Hülber, G. Klonner, D. Moser, M. Schütz, J. Wessely, W. Willner, N. E. Zimmermann, and S. Dullinger. 2018. Range dynamics of mountain plants decrease with elevation. Proceedings of the National Academy of Sciences 115:1848–1853.

Schall, P., M. M. Gossner, S. Heinrichs, M. Fischer, S. Boch, D. Prati, K. Jung, V. Baumgartner, S. Blaser, S. Böhm, F. Buscot, R. Daniel, K. Goldmann, K. Kaiser, T. Kahl, M. Lange, J. Müller, J. Overmann, S. C. Renner, E.-D. Schulze, J. Sikorski, M. Tschapka, M. Türke, W. W. Weisser, B. Wemheuer, T. Wubet, and C. Ammer. 2017. The impact of even-aged and uneven-aged forest management on regional biodiversity of multiple taxa in European beech forests. Journal of Applied Ecology.

Schelhaas, M.-J., G.-J. Nabuurs, and A. Schuck. 2003. Natural disturbances in the European forests in the 19th and 20th centuries. Global Change Biology 9:1620–1633.

Schigel, D. S. 2012. Fungivory and host associations of Coleoptera: a bibliography and review of research approaches. Mycology: An International Journal on Fungal Biology 3:258–272.

Schowalter, T. D. 2016. Insect Ecology: An Ecosystem Approach. Academic Press.

Schweiger, A. H., and C. Beierkuhnlein. 2015. Size dependency in color patterns of Western Palearctic carabids. Ecography 39:846–857.

Sebek, P., J. Altman, M. Platek, and L. Cizek. 2013. Is Active Management the Key to the Conservation of Saproxylic Biodiversity? Pollarding Promotes the Formation of Tree Hollows. PLOS ONE 8:e60456.

Sebek, P., R. Bace, M. Bartos, J. Benes, Z. Chlumska, J. Dolezal, M. Dvorsky, J. Kovar, O. Machac, B. Mikatova, M. Perlik, M. Platek, S. Polakova, M. Skorpik, R. Stejskal, M. Svoboda, F. Trnka, M. Vlasin, M. Zapletal, and L. Cizek. 2015. Does a minimal intervention approach threaten the biodiversity of protected areas? A multi-taxa short-term response to intervention in temperate oak-dominated forests. Forest Ecology and Management 358:80–89.

Segerer, A., A. Hausmann, G. Behounek, W. Speidel, and T. J. Witt. 2011. Die Großschmetterlinge Deutschlands. The Macrolepidoptera of Germany. First edition. Goecke & Evers, Budapest.

Seibold, S., C. Bässler, R. Brandl, B. Büche, A. Szallies, S. Thorn, M. D. Ulyshen, and J. Müller. 2016. Microclimate and habitat heterogeneity as the major drivers of beetle diversity in dead wood. Journal of Applied Ecology 53:934–943.

Seibold, S., C. Bässler, R. Brandl, L. Fahrig, B. Förster, M. Heurich, T. Hothorn, F. Scheipl, S. Thorn, and J. Müller. 2017. An experimental test of the habitat-amount hypothesis for saproxylic beetles in a forested region. Ecology 98:1613–1622.

Seibold, S., R. Brandl, J. Buse, T. Hothorn, J. Schmidl, S. Thorn, and J. Müller. 2015. Association of extinction risk of saproxylic beetles with ecological degradation of forests in Europe. Conservation Biology 29:382–390.

Seidl, R., D. C. Donato, K. F. Raffa, and M. G. Turner. 2016. Spatial variability in tree regeneration after wildfire delays and dampens future

bark beetle outbreaks. Proceedings of the National Academy of Sciences 113:13075–13080.

Seidl, R., D. Thom, M. Kautz, D. Martin-Benito, M. Peltoniemi, G. Vacchiano, J. Wild, D. Ascoli, M. Petr, J. Honkaniemi, M. J. Lexer, V. Trotsiuk, P. Mairota, M. Svoboda, M. Fabrika, T. A. Nagel, and C. P. O. Reyer. 2017. Forest disturbances under climate change. Nature Climate Change 7:395–402.

Sekar, S. 2012. A meta-analysis of the traits affecting dispersal ability in butterflies: can wingspan be used as a proxy? Journal of Animal Ecology 81:174–184.

Senf, C., D. Pflugmacher, Y. Zhiqiang, J. Sebald, J. Knorn, M. Neumann, P. Hostert, and R. Seidl. 2018. Canopy mortality has doubled in Europe's temperate forests over the last three decades. Nature Communications 9:4978.

Settele, J., R. Feldmann, and R. Reinhardt. 2000. Die Tagfalter Deutschlands. Ulmer, E, Stuttgart.

Shelomi, M. 2012. Where Are We Now? Bergmann's Rule Sensu Lato in Insects. The American Naturalist 180:511–519.

Shipley, B. 2004. Analysing the allometry of multiple interacting traits. Perspectives in Plant Ecology, Evolution and Systematics 6:235–241.

Shipley, B. 2007. Comparative Plant Ecology as a Tool for Integrating Across Scales. Annals of Botany 99:965–966.

Shipley, B. 2009. Confirmatory path analysis in a generalized multilevel context. Ecology 90:363–368.

Shipley, B. 2013. The AIC model selection method applied to path analytic models compared using a d-separation test. Ecology 94:560–564.

Shipley, B., F. De Bello, J. H. C. Cornelissen, E. Laliberté, D. C. Laughlin, and P. B. Reich. 2016. Reinforcing loose foundation stones in trait-based plant ecology. Oecologia 180:923–931.

Shipley, B., D. Vile, and É. Garnier. 2006. From Plant Traits to Plant Communities: A Statistical Mechanistic Approach to Biodiversity. Science 314:812–814.

Sibly, R. M., and D. Atkinson. 1994. How Rearing Temperature Affects Optimal Adult Size in Ectotherms. Functional Ecology 8:486–493.

Siemann, E., D. Tilman, and J. Haarstad. 1999. Abundance, diversity and body size: patterns from a grassland arthropod community. Journal of Animal Ecology 68:824–835.

Simons, N. K., M. M. Gossner, T. M. Lewinsohn, S. Boch, M. Lange, J. Müller, E. Pašalić, S. A. Socher, M. Türke, M. Fischer, and W. W. Weisser. 2014. Resource-Mediated Indirect Effects of Grassland Management on Arthropod Diversity. PLoS ONE 9:e107033.

Simons, N. K., M. M. Gossner, T. M. Lewinsohn, M. Lange, M. Türke, and W. W. Weisser. 2015. Effects of land-use intensity on arthropod species abundance distributions in grasslands. Journal of Animal Ecology 84:143–154.

Sinnott, R. W. 1984. Virtues of the haversine. Sky and Telescope 68:158–159.

Snäll, T., and B. G. Jonsson. 2001. Edge Effects on Six Polyporous Fungi Used as Old-Growth Indicators in Swedish Boreal Forest. Ecological Bulletins:255–262.

Sober, E. 2000. Philosophy of Biology, 2nd Edition. 2nd edition. Perseus, Boulder, Colo.

Socher, S. A., D. Prati, S. Boch, J. Müller, H. Baumbach, S. Gockel, A. Hemp, I. Schöning, K. Wells, F. Buscot, E. K. V. Kalko, K. E. Linsenmair, E.-D. Schulze, W. W. Weisser, and M. Fischer. 2013. Interacting effects of fertilization, mowing and grazing on plant species diversity of 1500 grasslands in Germany differ between regions. Basic and Applied Ecology 14:126–136.

Socher, S. A., D. Prati, S. Boch, J. Müller, V. H. Klaus, N. Hölzel, and M. Fischer. 2012. Direct and productivity-mediated indirect effects of fertilization, mowing and grazing on grassland species richness. Journal of Ecology 100:1391–1399.

Soininen, J., R. McDonald, and H. Hillebrand. 2007. The distance decay of similarity in ecological communities. Ecography 30:3–12.

Sommerfeld, A., C. Senf, B. Buma, A. W. D'Amato, T. Després, I. Díaz-Hormazábal, S. Fraver, L. E. Frelich, Á. G. Gutiérrez, S. J. Hart, B. J. Harvey, H. S. He, T. Hlásny, A. Holz, T. Kitzberger, D. Kulakowski, D. Lindenmayer, A. S. Mori, J. Müller, J. Paritsis, G. L. W. Perry, S. L. Stephens, M. Svoboda, M. G. Turner, T. T. Veblen, and R. Seidl. 2018. Patterns and drivers of recent disturbances across the temperate forest biome. Nature Communications 9:4355.

Speight, M. C. D. 1989. Saproxylic invertebrates and their conservation. Nature and Environment Series (UK).

Stein, A., and H. Kreft. 2015. Terminology and quantification of environmental heterogeneity in species-richness research. Biological Reviews 90:815–836.

Steiner, A., U. Ratzel, M. Top-Jensen, and M. Fibiger. 2014. Die Nachtfalter Deutschlands - Ein Feldführer. BugBook Publishing, Oesternmarie, Denmark.

Stelbrink, P., S. Pinkert, S. Brunzel, J. Kerr, C. W. Wheat, R. Brandl, and D. Zeuss. 2019. Color lightness of butterfly assemblages across North America and Europe. Scientific Reports 9:1760.

Stephens, P. A., I. L. Boyd, J. M. McNamara, and A. I. Houston. 2009. Capital breeding and income breeding: their meaning, measurement, and worth. Ecology 90:2057–2067.

Stevens, V. M., A. Trochet, H. V. Dyck, J. Clobert, and M. Baguette. 2012. How is dispersal integrated in life histories: a quantitative analysis using butterflies. Ecology Letters 15:74–86.

Stokland, J. N., J. Siitonen, and B. G. Jonsson. 2012. Biodiversity in dead wood. Cambridge University Press.

Suzuki, Y., and H. F. Nijhout. 2008. Genetic basis of adaptive evolution of a polyphenism by genetic accommodation. Journal of Evolutionary Biology 21:57–66.

Svenning, J.-C., C. Fløjgaard, and A. Baselga. 2011. Climate, history and neutrality as drivers of mammal beta diversity in Europe: insights from multiscale deconstruction. Journal of Animal Ecology 80:393–402.

Svenning, J.-C., S. Normand, and F. Skov. 2008. Postglacial dispersal limitation of widespread forest plant species in nemoral Europe. Ecography 31:316–326.

Swanson, M. E., J. F. Franklin, R. L. Beschta, C. M. Crisafulli, D. A. DellaSala, R. L. Hutto, D. B. Lindenmayer, and F. J. Swanson. 2011. The

forgotten stage of forest succession: early-successional ecosystems on forest sites. Frontiers in Ecology and the Environment 9:117–125.

Tabaku, V. 2000. Struktur von Buchen-Urwäldern in Albanien im Vergleich mit deutschen Buchen-Naturwaldreservaten und-Wirtschaftswäldern. PhD Thesis, Universität Göttingen, Göttingen.

Tales, E., P. Keith, and T. Oberdorff. 2004. Density-range size relationships in French riverine fishes. Oecologia 138:360–370.

Talloen, W., H. Van Dyck, and L. Lens. 2004. The Cost of Melanization: Butterfly Wing Coloration under Environmental Stress. Evolution 58:360–366.

Tammaru, T., and E. Haukioja. 1996. Capital Breeders and Income Breeders among Lepidoptera: Consequences to Population Dynamics. Oikos 77:561–564.

Tamura, K., D. Peterson, N. Peterson, G. Stecher, M. Nei, and S. Kumar. 2011. MEGA5: Molecular Evolutionary Genetics Analysis Using Maximum Likelihood, Evolutionary Distance, and Maximum Parsimony Methods. Molecular Biology and Evolution 28:2731–2739.

Tepley, A. J., F. J. Swanson, and T. A. Spies. 2013. Fire-mediated pathways of stand development in Douglas-fir/western hemlock forests of the Pacific Northwest, USA. Ecology 94:1729–1743.

Thom, D., W. Rammer, T. Dirnböck, J. Müller, J. Kobler, K. Katzensteiner, N. Helm, and R. Seidl. 2017. The impacts of climate change and disturbance on spatio-temporal trajectories of biodiversity in a temperate forest landscape. Journal of Applied Ecology 54:28–38.

Thomas, C. D., and P. K. Gillingham. 2015. The performance of protected areas for biodiversity under climate change. Biological Journal of the Linnean Society 115:718–730.

Thünen-Institut, Z. B. 2012. Ergebnisdatenbank, https://bwi.info, 77Z1JI_L221of_2012.

Thunes, K. H., and E. Willassen. 1997. Species composition of beetles (Coleoptera) in the bracket fungi Piptoporus betulinus and Fomes fomentarius (Aphyllophorales: Polyporaceae): an explorative approach with canonical correspondence analysis. Journal of Natural History 31:471–486.

Tiede, Y., C. Hemp, A. Schmidt, T. Nauss, N. Farwig, and R. Brandl. 2018. Beyond body size: consistent decrease of traits within orthopteran assemblages with elevation. Ecology 99:2090–2102.

Tikkanen, O.-P., T. Heinonen, J. Kouki, and J. Matero. 2007. Habitat suitability models of saproxylic red-listed boreal forest species in long-term matrix management: Cost-effective measures for multi-species conservation. Biological Conservation 140:359–372.

Tiple, A. D., A. M. Khurad, and R. L. H. Dennis. 2009. Adult butterfly feeding-nectar flower associations: constraints of taxonomic affiliation, butterfly, and nectar flower morphology. Journal of Natural History 43:855–884.

Tolman, T., and R. Lewington. 2008. Collins Butterfly Guide: The Most Complete Field Guide to the Butterflies of Britain and Europe. 3rd edition. HarperCollins UK, London.

Tonkin, J. D., F. O. Arimoro, and P. Haase. 2016. Exploring stream communities in a tropical biodiversity hotspot: biodiversity, regional occupancy, niche characteristics and

environmental correlates. Biodiversity and Conservation 25:975–993.

True, J. R. 2003. Insect melanism: the molecules matter. Trends in Ecology & Evolution 18:640–647.

Umbers, K. D. L., M. E. Herberstein, and J. S. Madin. 2013. Color in insect thermoregulation: Empirical and theoretical tests in the color-changing grasshopper, Kosciuscola tristis. Journal of Insect Physiology 59:81–90.

Urbanek, S. 2013. png: Read and write PNG images. R package version 0.1-7.

Utrio, P. 1995. On flight temperatures and foraging strategies of nocturnal moths. Baptria 20:113–122.

Vainio, L., H. Hakkarainen, M. J. Rantala, and J. Sorvari. 2004. Individual variation in immune function in the ant Formica exsecta; effects of the nest, body size and sex. Evolutionary Ecology 18:75–84.

Välimäki, P., S. M. Kivelä, J. Raitanen, V.-M. Pakanen, E. Vatka, M. I. Mäenpää, N. Keret, and T. Tammaru. 2015. Larval melanism in a geometrid moth: promoted neither by a thermal nor seasonal adaptation but desiccating environments. Journal of Animal Ecology 84:817–828.

Vandekerkhove, K., L. De Keersmaeker, R. Walleyn, F. Köhler, L. Crevecoeur, L. Govaere, A. Thomaes, and K. Verheyen. 2012. Reappearance of old growth elements in lowland woodlands in northern Belgium: do the associated species follow? SILVA FENNICA 45:909–935.

Vanonckelen, S., and A. V. Rompaey. 2015. Spatiotemporal Analysis of the Controlling Factors of Forest Cover Change in the Romanian Carpathian Mountains. Mountain Research and Development 35:338–351.

Vellend, M. 2010. Conceptual Synthesis in Community Ecology. The Quarterly Review of Biology 85:183–206.

Vellend, M. 2016. The Theory of Ecological Communities. MPB Series: 57. Princeton University Press, Princeton.

Venier, L. A., and L. Fahrig. 1996. Habitat Availability Causes the Species Abundance-Distribution Relationship. Oikos 76:564–570.

Venier, L. A., and L. Fahrig. 1998. Intra-Specific Abundance-Distribution Relationships. Oikos 82:483–490.

Verberk, W. C. E. P., G. Van Der Velde, and H. Esselink. 2010. Explaining abundance–occupancy relationships in specialists and generalists: a case study on aquatic macroinvertebrates in standing waters. Journal of Animal Ecology 79:589–601.

Vilén, T., K. Gunia, P. J. Verkerk, R. Seidl, M.-J. Schelhaas, M. Lindner, and V. Bellassen. 2012. Reconstructed forest age structure in Europe 1950–2010. Forest Ecology and Management 286:203–218.

Violle, C., M.-L. Navas, D. Vile, E. Kazakou, C. Fortunel, I. Hummel, and E. Garnier. 2007. Let the concept of trait be functional! Oikos 116:882–892.

Violle, C., P. B. Reich, S. W. Pacala, B. J. Enquist, and J. Kattge. 2014. The emergence and promise of functional biogeography. Proceedings of the National Academy of Sciences 111:13690–13696.

Wachmann, E., A. Melber, and J. Deckert. 2004. Wanzen Band 2: Cimicomorpha:

Microphysidae (Flechtenwanzen), Miridae (Weichwanzen). First edition. Goecke & Evers.

Wachmann, E., A. Melber, and J. Deckert. 2006. Wanzen, Band 1: Dipsocoromorpha, Nepomorpha, Gerromorpha, Leptopodomorpha, Cimicomorpha. First edition. Goecke & Evers.

Wachmann, E., A. Melber, and J. Deckert. 2007. Wanzen, Band 3: Pentatomomorpha I: Aradidae, Lygaeidae, Piesmatidae, Berytidae, Pyrrhocoridae, Alydidae, Coreidae, Rhopalidae, Stenocephalidae. First edition. Goecke & Evers.

Wachmann, E., A. Melber, and J. Deckert. 2008. Wanzen, Band 4. Pentatomomorpha II: Pentatomoidea: Cydnidae, Thyreocoridae, Plataspidae, Acanthosomatidae, Scutelleridae, Pentatomidae. First edition. Goecke & Evers.

Wachmann, E., A. Melber, and J. Deckert. 2012. Wanzen Band 5: Supplementband. Dipsocoromorpha, Nepomorpha, Gerromorpha, Leptopodomorpha, Cimicomorpha und Pentatomomorpha. First edition. Goecke & Evers.

Wagner, G. K., and R. Gosik. 2016. Comparative morphology of immature stages of two sympatric Tenebrionidae species, with comments on their biology. Zootaxa 4111:201–222.

Wahlberg, N., N. Snäll, J. Viidalepp, K. Ruohomäki, and T. Tammaru. 2010. The evolution of female flightlessness among Ennominae of the Holarctic forest zone (Lepidoptera, Geometridae). Molecular Phylogenetics and Evolution 55:929–938.

Walsh, C., and R. Mac Nally. 2013. hier.part: Hierarchical Partitioning. R package version 1.0-4.

Watt, W. B. 1968. Adaptive Significance of Pigment Polymorphisms in Colias Butterflies. I. Variation of Melanin Pigment in Relation to Thermoregulation. Evolution 22:437–458.

Webb, C. O., D. D. Ackerly, M. A. McPeek, and M. J. Donoghue. 2002. Phylogenies and Community Ecology. Annual Review of Ecology and Systematics 33:475–505.

White, E. P., S. K. M. Ernest, A. J. Kerkhoff, and B. J. Enquist. 2007. Relationships between body size and abundance in ecology. Trends in Ecology & Evolution 22:323–330.

Wiens, J. A., J. T. Rotenberry, and B. Van Horne. 1987. Habitat Occupancy Patterns of North American Shrubsteppe Birds: The Effects of Spatial Scale. Oikos 48:132–147.

Williams, P. 2001. WorldMap software. Natural History Museum, London.

Willner, W., R. Di Pietro, and E. Bergmeier. 2009. Phytogeographical evidence for post-glacial dispersal limitation of European beech forest species. Ecography 32:1011–1018.

Wilson, K., S. C. Cotter, A. F. Reeson, and J. K. Pell. 2001. Melanism and disease resistance in insects. Ecology Letters 4:637–649.

Wisskirchen, R., and H. Haeupler. 1998. Standardliste der Farn-und Blütenpflanzen Deutschlands. Verlag Eugen Ulmer, Stuttgart.

Wright, D. H. 1983. Species-Energy Theory: An Extension of Species-Area Theory. Oikos 41:496–506.

Xing, S., T. C. Bonebrake, L. A. Ashton, R. L. Kitching, M. Cao, Z. Sun, J. C. Ho, and A. Nakamura. 2018. Colors of night: climate–morphology relationships of geometrid moths along spatial gradients in southwestern China. Oecologia 188:537–546.

Yao, W., P. Krzystek, and M. Heurich. 2012. Tree species classification and estimation of stem volume and DBH based on single tree extraction by exploiting airborne full-waveform LiDAR data. Remote Sensing of Environment 123:368–380.

Yin, H., Q. Shi, M. Shakeel, J. Kuang, and J. Li. 2016. The Environmental Plasticity of Diverse Body Color Caused by Extremely Long Photoperiods and High Temperature in Saccharosydne procerus (Homoptera: Delphacidae). Frontiers in Physiology 7.

Zehetgruber, B., J. Kobler, T. Dirnböck, R. Jandl, R. Seidl, and A. Schindlbacher. 2017. Intensive ground vegetation growth mitigates the carbon loss after forest disturbance. Plant and Soil:1–14.

Zellweger, F., T. Roth, H. Bugmann, and K. Bollmann. 2017. Beta diversity of plants, birds and butterflies is closely associated with climate and habitat structure. Global Ecology and Biogeography 26:898–906.

Zenner, E. K., J. E. Peck, M. L. Hobi, and B. Commarmot. 2016. Validation of a classification protocol: meeting the prospect requirement and ensuring distinctiveness when assigning forest development phases. Applied Vegetation Science 19:541–552.

Zeuss, D., R. Brandl, M. Brändle, C. Rahbek, and S. Brunzel. 2014. Global warming favours light-colored insects in Europe. Nature Communications 5.

Zeuss, D., S. Brunzel, and R. Brandl. 2017. Environmental drivers of voltinism and body size in insect assemblages across Europe. Global Ecology and Biogeography 26:154–165.

Zhang, C.-Y., J.-Y. Meng, X.-P. Wang, F. Zhu, and C.-L. Lei. 2011. Effects of UV-A exposures on longevity and reproduction in Helicoverpa armigera, and on the development of its F1 generation. Insect Science 18:697–702.

Zuur, A. F., E. N. Ieno, and C. S. Elphick. 2010. A protocol for data exploration to avoid common statistical problems. Methods in Ecology and Evolution 1:3–14.

Zuur, A., E. N. Ieno, N. Walker, A. A. Saveliev, and G. M. Smith. 2009. Mixed Effects Models and Extensions in Ecology with R. 2009th edition. Springer, New York, NY.

Zytynska, S. E., I. Doerfler, M. M. Gossner, S. Sturm, W. W. Weisser, and J. Müller. 2018. Minimal effects on genetic structuring of a fungus-dwelling saproxylic beetle after recolonisation of a restored forest. Journal of Applied Ecology 55:2933–2943.

Danksagung

Es gibt eine ganze Reihe von Menschen ohne die diese Arbeit nicht möglich gewesen wäre. Angefangen mit den Lehrenden am Fachbereich Biologie, die mir seit Beginn meines Bachelors einiges über die wunderbar komplexe Welt der Biologie beigebracht haben. Hierbei hatte ich das Glück von einigen herausragenden Professorinnen und Professoren sowie Dozentinnen und Dozenten lernen zu dürfen. Ganz vorneweg möchte ich Dir, Roland Brandl, besonders danken. Kein anderer Mensch hat mein Denken so geprägt wie Du. Du brachtest mich zur Weißglut, zum Verzweifeln und zum Wahnsinn, aber auch zum Nachdenken, zum Erkennen und zum Lachen. Deine Unterstützung in allen Lebenslagen hat mir trotz der prekären Arbeitssituation die nötige Sicherheit gegeben um mich entfalten zu können. Abgesehen von Roland wurde mein Weg durch Martin Brändle und seine stete Förderung und seine Einflussnahme an einigen wichtigen Punkten in meinem Leben maßgeblich beeinflusst: von ihm bekam ich den ersten Job als studentische Hilfskraft, er vermittelte mir die ökologische Bedeutung der Arthropoden, er betreute meine Bachelor- und Masterarbeiten, er nahm mich mit zu meiner ersten wissenschaftlichen Tagung, er fuhr mit mir in den Nationalpark Bayerischer Wald um mir dort (erfolgreich) eine Möglichkeit zur Promotion zu verschaffen und er sorgte sogar dafür das ich nach der Promotion direkt eine Weiterbeschäftigung habe. Neben diesen „Karrieremaßnahmen“ stand er auch immer bereit um mit mir ökologische Fragestellungen zu diskutieren und hatte immer das nötige Paper parat, wenn ich mal nicht weiterkam. Für all das möchte ich Dir, lieber Martin, ganz herzlich danken. Besonderer Dank gilt natürlich auch dem Rest der Arbeitsgruppe. Ich danke Stefan Pinkert, Lea Heidrich, Roman Fricke und Dirk Zeuss für die spannenden und witzigen Diskussionen zu wissenschaftlichen und unwissenschaftlichen Themen im Raucherbereich der AG. Außerdem danke ich Lars Opgenoorth für die vergangene und hoffentlich zukünftige Zusammenarbeit und Stefan Hotes für seine Geduld mit den lauten Kollegen im Nachbarbüro und natürlich seine Zusammenarbeit in Waldfragen. Weiterhin danke ich Antje Schmidt, Juliane Röder, Sascha Rösner, Daniel Acquah-Lamptey und allen anderen die das Arbeitsumfeld so wundervoll gestaltet haben. Ebenso bin ich Nina Farwig und ihrer Arbeitsgruppe zu großem Dank verpflichtet. Von Nina und Dana Schabo habe ich über die Jahre eine Menge über den praktischen und wissenschaftlichen Naturschutz lernen dürfen und hatte über die beiden die Möglichkeit eine wunderbare Zeit im Białowieża-Urwald zu verbringen.

Diese Arbeit wäre außerdem nicht möglich gewesen ohne die finanzielle Unterstützung der Rudolf-und-Helene-Glaser Stiftung organisiert im Stifterverband für die deutsche

Wissenschaft. Das Promotionsstipendium ermöglichte mir die fruchtbare Zusammenarbeit mit dem Nationalpark Bayerischer Wald und gab mir den nötigen Freiraum mich zu entfalten.

Meine Zeit im Nationalpark Bayerischer Wald war extrem arbeits- und lehrreich und ich möchte Dr. Franz Leibl für die Möglichkeit an diesem besonderen Ort zu arbeiten sowie allen MitarbeiterInnen der Nationalparkverwaltung und der Nationalparkwacht für die Unterstützung danken. Speziell bedanken möchte ich mich beim Sachgebiet III mit Claus Bässler, Linda Seifert, Marco Heurich, Helmut Hackl, Josef Nusshardt, Claudia Schmidt und Burkhard Beudert für die tolle Zusammenarbeit. Hierbei gilt ganz besonderer Dank Prof. Dr. Jörg Müller der maßgeblich zu meinem Verständnis des Ökosystems Wald beigetragen hat und der mir mit seiner unnachahmlichen Art einiges über praktischen und wissenschaftlichen Naturschutz beigebracht hat. Seine Ausdauer, seine (Denk-)Geschwindigkeit und sein Talent Menschen zusammen zu bringen haben mich immer fasziniert.

Weiterhin möchte ich meinen Ko-Doktoranden im Walddienst Torben Hilmers und Jonas Hagge für die wunderbare Zusammenarbeit danken, die hoffentlich in Zukunft weiter fortgeführt wird. Wir haben den Wald gehörig aufgeräumt und können mächtig stolz sein auf das was wir dort gemeinsam bewerkstelligt haben. All das wäre allerdings nicht möglich gewesen ohne die tatkräftige Unterstützung die wir im Wald hatten. In der Hoffnung niemand vergessen zu haben möchte ich Anja Schulze-Bierbach, Paul Hertlein, Julia Hetzl, Johannes Mader, Christopher Meyer, Bernhard Depner, Volker Schmück, Kathrin Möhrle, Jonas Rochlitz, Theresia Endriß, Sophie Belval, Hanna Nagl, Kranti Navarre, Stefanie Batke, Andrès Geist, Kim Fasse, Sarina Thiel, Jorina Fink, Alexander Drexler, Joe Premier, Antje Heideroth, Moritz Waas, Leo Christoph, Marion Dorsch und Katharina Scharf für die Zusammenarbeit und die spannende und lustige Zeit im Nationalpark danken. Dabei möchte ich außerdem Simon Thorn und Sebastian Seibold für die Vorarbeit, die sie im Nationalpark geleistet haben, danken von der wir ebenso wie von ihrer persönlichen Unterstützung bei der Arbeit im Nationalpark ständig profitiert haben. Für die Bearbeitung der Unmengen an Arthropodenproben gilt mein Dank den vielen ExpertInnen die mir mit Rat und Tat zur Seite standen: Martin Goßner (Wanzen), Herbert Nickel (Zikaden), Gisela Merkel-Wallner (Schwebfliegen), Jörg Salamon (Springschwänze), Hermann Hacker (Nachtfalter), Boris Büche und Alex Szallies (Käfer), Christian Schmid-Egger (Stechimmen), Andrew Liston (Pflanzenwespen) und Ingmar Weiß (Spinnen).

Ich danke meinen tollen Freunden die mich in den Kneipen Marburgs und der Welt immer wieder auf andere Gedanken brachten und wo es statt um Ökologie, Naturschutz und Insekten Gott sei Dank auch mal um Punkrock, Angeln und Videospiele ging. Ich danke meiner Familie mit meiner Schwester Julia, meinem Onkel Thomas und meiner Mutter Ursula die mich mein gesamtes Leben unterstützt haben und ohne die ich natürlich absolut nicht da wäre wo ich bin. Ich danke der erweiterten Familie Spatz und den dazugehörigen Anhängen für die vielen entspannten Wochenenden im Garten die mir den nötigen Ausgleich gaben.

Ganz besonderer Dank gilt meiner eigenen frisch-gebackenen Familie. Lennard ich danke Dir fürs gemeinsame Faust-Lesen und Deine fanatische Liebe zu Tigger und Winnie Pooh. Ella Marie ich danke Dir fürs gemeinsame Tanzen und die vielen irren Geschichten die Du mir schon erzählt hast. Euer Lachen gibt mir unendlich viel Kraft. Ich danke Euch beiden dafür, dass ihr mir gezeigt habt was wichtig ist im Leben und dass ihr mir einen Grund gebt jeden Tag mein Bestes zu geben. Theresa ich danke Dir für die Kraft die Du mir gibst und die Geduld die Du mit mir hast. Ich danke Dir dafür, dass Du mich wieder hochziehst, wenn ich am Boden liege und dass Du mich runterholst, wenn ich zu hochfliege. Ich danke Dir für jede Minute die wir zusammen verbracht haben, für jeden Ort den wir zusammen gesehen haben und für all das was noch kommen wird. Ihr drei Spatzen seid der Mittelpunkt meines Lebens und ich liebe Euch von Herzen.

Erklärung

Erklärung

Hiermit versichere ich, dass ich meine Dissertation mit dem Titel

„Population and community responses along environmental gradients across spatio-temporal scales“

selbständig und ohne unerlaubte Hilfe verfasst habe. Ich habe mich keiner als der in ihr angegebenen Quellen oder Hilfsmittel bedient und alle vollständig oder sinngemäß übernommenen Zitate als solche gekennzeichnet. Diese Dissertation wurde in der vorliegenden oder einer ihr ähnlichen Form noch bei keiner anderen in- oder ausländischen Hochschule eingereicht und hat noch keinen sonstigen Prüfungszwecken gedient.

Unterschrift (Nicolas Alexander Konstantin Frieß)

Marburg, März 2018